

**EFFECTS OF INTRODUCED MOOSE (*Alces alces*) ON VEGETATION  
COMPOSITION, NUTRIENT DYNAMICS, AND DECOMPOSITION RATES IN  
BOREAL FOREST ECOSYSTEMS IN NEWFOUNDLAND, CANADA**

by

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## **ABSTRACT**

Globally, consumers affect ecosystem processes including nutrient dynamics. Herbivores have been known to slow nutrient flow in boreal forest ecosystems. I examined the effects of introduced moose on disturbed forests of Newfoundland, Canada by conducting a field experiment during August - November 2014 in 20 paired moose exclosure-control plots. I tested whether moose browsing directly and indirectly affected forests by measuring plant species composition, litter quality and quantity, soil quality, and decomposition rates in areas moose exclosure-control plots. I analyzed moose effects using linear mixed effects models and found evidence indicating that moose reduce plant height and litter biomass affecting the availability of carbon, nitrogen, and phosphorus. However, plant diversity, soil quality, and litter decomposition did not differ between moose exclosures and controls. Moose in Newfoundland directly influence plant regeneration and litter biomass while indirect effects on soil ecosystems may be limited by time, disturbance, and climate.

## **DEDICATION**

I dedicate my master's thesis to my grandfather, Dr. Robert C. Ellis, who completed his master's on forest regeneration in Newfoundland, and whose research I have had the privilege to build on and share with him.

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## **CHAPTER 1: General Introduction**

### **1.1. Ecological stoichiometry and consumers: theory and background**

Ecological stoichiometry defines ecological processes using a suite of elements relating organism function to their elemental composition (Sternner & Elser 2002). Organisms use a suite of 25 elements that are essential to life (Sternner & Elser 2002). The quantity and ratio of elements, particularly carbon, nitrogen, and phosphorus, affects resource production and limitation, nutrient cycling, and trophic interactions (Elser et al. 2000b). Carbon, nitrogen, and phosphorus are important elements for biological structural molecules (Sternner & Elser 2002). For example, carbon accounts for approximately 40 – 50 % of dry biomass of most living things (Sternner & Elser 2002). Labile carbon is an important source of energy and is easily measured with other elements in organic tissue (Hessen et al. 2004). Nitrogen and phosphorus are important elements for the growth of all individuals. For example, phosphorus is associated with the production of ribosomal RNA required for protein synthesis (Elser et al. 2000a) and is also a source of energy required for cells (Bracken et al. 2014), while nitrogen plays a key role in the synthesis of proteins (Sternner & Elser 2002).

Within ecosystems, these elemental concentrations vary along environmental gradients, among growth forms and evolutionary lineages, and are dependent on nutrient supply (Borer et al. 2013; Martiny et al. 2013). In plants, for example, the distribution of elements differs between angiosperms and gymnosperms, and deciduous and coniferous plants. The distribution of elements also varies among different parts of plants (Stone et al. 1979); for example, photosynthetic material has a higher concentration of nitrogen per

unit dry mass than stems or roots (Sturner & Elser 2002). The elemental contents of plant species play an important role in a number of ecosystem processes including plant growth, litter decomposition, resource limitations, and herbivory (Hobbie 1992; Cebrian 1999; Borer et al. 2013). For example, Ellis and Pennington (1988) found that the rate of nitrification in soils in Tasmania, Australia was dependent on the presence of specific tree species, with the highest nitrification rates occurring in temperate rainforest.

The stoichiometry of plants mediates food web dynamics by affecting consumer feeding behaviour, population stability, and community organization (Elser et al. 2000a.). Consumers require nitrogen and phosphorus from a lower trophic level to obtain the elements required for maintaining fitness and reproduction of individuals to sustain species populations. Stoichiometric variation is very plastic among autotrophic species, while the stoichiometry of consumers tends to be bounded within a narrow range (Hessen et al. 2004). For example, a global meta-analysis by Elser et al. (2000b) report a mean ( $\pm$  sd) C:N ratio of terrestrial autotrophs as 36 ( $\pm$  23), while the mean ( $\pm$  sd) C:N of terrestrial invertebrate herbivores as 6.5 ( $\pm$  1.9). As a result, consumers have to decide how to i) acquire resources (DeGabriel et al. 2013); and ii) assimilate elements based on elemental requirements (McIntyre & Flecker 2010; Schmitz et al. 2010). Preferential consumption of plant material can change plant species composition ultimately leading to changes in the stoichiometric balance of the environment.

I set out to examine how selective feeding by an introduced herbivore affects ecological stoichiometry in the boreal forest of the island of Newfoundland, Canada.

## **1.2. Herbivores as drivers of succession and key ecosystem processes**

Herbivore feeding preferences can influence the biomass, abundance, and dynamics of species throughout ecosystems. Litter palatability, quality, and decomposition are related interspecifically across plant species; therefore, herbivore feeding has the potential to cause changes in the relative abundance of preferred and non-preferred plant species causing variation in the quality of litter produced thereby impacting decomposer activity (Wardle et al. 2002). Selective herbivory can alter community structure changing the quantity and chemical quality of litter returned to the soil, thereby altering soil nutrient availability and ultimately affecting whole ecosystem nutrient cycles (Pastor & Naiman 1992). Results from a number of studies have indicated that foliar herbivores have the capacity to alter key belowground processes through changes in plant communities (see Table 1.1) (Wardle et al. 2002), having either positive or negative effects on soil ecosystems depending on whether they are grazers or browsers (Ayres et al. 2004).

Grazers' diet consists of monocotyledons such as grasses and forbs (Fritz & Loison 2006). Herbivory by grazers, such as bison and sheep, typically decelerate succession. Grazers can increase compensatory growth when those selected species tolerate grazing (Wardle et al. 2004; Hester et al. 2006). Grazing optimization theory states that primary productivity increases with higher feeding rates and plateaus under moderate herbivory (McNaughton 1979; De Mazancourt et al. 1999). Grazing can stimulate dominance of preferred plant species through increased nutrient uptake, faster growth rates in remaining plant components, and higher tissue nutrient concentration (Leriche et al. 2001). There is empirical support for the grazing optimization theory; for

example, Bazely and Jeffries (1986) found grazing by lesser snow geese (*Anser caerulescens caerulescens*) in Manitoba, Canada increased compensatory growth in grazed graminoids escalating net aboveground primary productivity. In range lands, grasslands and savannahs, this mechanism of increased productivity alters the trajectory of succession, by limiting growth of later successional species (Harrison & Bardgett 2004). As a result of nutrient rich regrowth and early successional species, litter fall is rich in nitrogen and readily labile, resulting in a low carbon: nitrogen ratio in soil where herbivores are grazing (Olofsson & Oksanen 2002).

Unlike grazers, browsers tend to accelerate succession and limit nutrient cycling (Côte et al. 2004; Bressette et al. 2012). Browsers, such as white tailed deer and moose, select dicotyledons, particularly nutrient rich woody species (Fritz & Loison 2006), resulting in a community shift towards poor quality plant material (Brandner et al. 1990; van Cleve et al. 1991; Rossow et al. 1997; DeJager and Pastor 2009). Nutrient poor plant species are able to outcompete nutrient rich plant species for a number of reasons. First, nutrient rich species growth is stunted by herbivory as photosynthetic plant tissue is consumed (Brandner et al. 1990; Butler & Kielland 2007), while photosynthetic plant tissue in unpalatable species is left largely unbrowsed (Burney & Jacobs 2013). Secondly, nutrient poor species are able to grow under nutrient limitation (Bryant et al. 1983). Climax species, such as black spruce (*Picea mariana*), are rich in lignins and tannins, defence compounds that make needles unpalatable. Lignins and tannins make litter recalcitrant, and when needles are deposited to the forest floor decomposition is slowed and nutrients, particularly nitrogen, becomes scarce (van Cleve et al. 1991; Ritchie et al. 1998).



### **1.3. Introduction of moose to Newfoundland, Canada**

Newfoundland, an island off the east coast of Canada, is comprised of boreal forest and barrens (Joyce & Mahoney 2001). Newfoundland's climate is wet, with approximately 1000 mm of precipitation annually, and a short growing season. On average, Newfoundland experiences approximately 115-145 days between first and last frost but many of these days do not reach the minimum temperatures required for plant growth (Government of Canada 2015). The island experienced a number of ice ages, the last occurring approximately 19,000 years ago (Rogerson 1983). As the ice receded 18,000 years BP, the landscape was stripped of vegetation and soil and was recolonized shortly thereafter, resulting in limited floral and faunal diversity (Rogerson 1983). For example, Newfoundland has fewer terrestrial mammals than areas of mainland North America at similar latitudes (Dodds 1983). Of 26 mammalian species occurring on the island, only 13 are native while the remaining 13 are non-native or transient (Strong & Leroux 2014).

An introduced species of particular concern for the ecology of Newfoundland is moose (*Alces alces*). Two individuals were introduced in 1878 from Nova Scotia, followed by a second introduction of four moose from New Brunswick in 1905 (Pimlott 1953). Since then the population of moose grew to 150,000 individuals during 1988 – 1992 (Joyce & Mahoney 2001). The population growth of moose can be attributed to three factors: little competition, absence of disease (Strong & Leroux 2014), and lack of predation (Pimlott 1959). Moose in Newfoundland exist at the highest densities (between 0.41 to 7.0 moose/km<sup>2</sup> (Joyce & Mahoney 2001)) compared to the rest of North America

(Karns 1998). For example, in 1999, Crête and Daigle estimated that moose densities in Newfoundland averaged tenfold higher than parts of their native range in North America.

A dramatic increase in moose populations can cause dramatic changes in plant communities. A significant portion of research on moose effects has occurred in Isle Royale, Alaska, and Scandinavia (Table 1.1). Researchers on Isle Royale found that balsam fir dominant stands were being converted to white and black spruce dominant forests under moderate and high moose density (Pastor et al. 1988; McInnes et al. 1992; DeJager & Pastor 2009). Kielland and Byrant (1998) found moose browsing in Alaska accelerates vegetation turnover from willow to alder. Similar trends have been found in balsam fir stands in Newfoundland. For example, in 1960, Ellis found that previously logged balsam fir stands near Badger, Newfoundland changed to black spruce under continuous moose browsing. Reports continue to describe damage to white birch and balsam fir across the island as a result of browsing (Ellis 1960; Bergerud & Manuel 1968; Thompson et al. 1992; Thompson and Curran 1993; McLaren et al. 2000; Tabuchi et al. 2011). Studies have also demonstrated some cascading effects to other biota. Gosse et al. (2011) found that seedbeds below balsam fir are shifting from feathermoss to grasses and non-native plants in Gros Morne National Park (GMNP). Thompson and Mallik (1989) found exclusion of moose reduced the growth of sheep laurel (*Kalmia angustifolia*) but moose browsing increased the dominance of sheep laurel inhibiting the growth of regeneration coniferous species. Connor et al. (2000) found that species diversity in GMNP declined from 1977 to 1996 under increasing moose density. Changes in plant composition as a result of moose browsing have been found to impact bird (Rae et al. 2013) and insect (Tabuchi et al. 2011) communities. However, unlike research elsewhere,

studies in Newfoundland have not focused on the cascading effects of moose on soils or key ecosystem processes, such as nutrient cycling and decomposition.

Parks Canada is concerned with the effects of the large moose population on forest ecology in Newfoundland as the introduced population has negatively affected the structure, function, and native diversity of forests on the island (Parks Canada 2013). In the 1970's, Terra Nova National Park (TNNP) experienced a massive insect infestation that dramatically impacted the forests in the park and the large moose population is impairing the natural regeneration of these insect disturbed forests. After consultation with the public, Parks Canada implemented hunting in GMNP and TNNP in 2011. Of 45 Canadian national parks, GMNP and TNNP are two of three that allow hunting for non-traditional purposes (Parks Canada, personal communication), issuing 3% of the total moose hunting tags in Newfoundland (Newfoundland and Labrador 2014). From 2011 - 2014, approximately 80 moose were been removed from TNNP through hunting. Similarly, it has been proposed that a non-traditional moose hunt begin in Cape Breton Highlands National Park due to similar ecological impacts of the large, but native moose population.

#### **1.4. Thesis overview**

I set out to examine how introduced moose influence boreal forest ecosystems in Newfoundland to determine if patterns of browser effects on forests are ubiquitous or if climate and abiotic conditions alter the expression of ungulate effects. This represents a novel study as Newfoundland has different climatic, biological, and disturbance history than previous research (Table 1.1). My objectives were to describe the direct influence of

moose browsing on plant community composition and if moose indirectly influence plant litter quality and quantity, soil quality, and litter decomposition rates. In Chapter 2, I conducted a field study using 10 established moose exclosure/reference pairs set up in 1995 and 1998 in previously disturbed forests to examine moose effects on nutrient cycling in the forests of Newfoundland, Canada. After approximately 20 years of the exclusion of moose, we found moose browse did limit plant height and plant litter biomass. However, we found no difference in plant species diversity, soil quality, or litter decomposition rates.

## **1.5. References**

- Ayres, E., J. Heath, M. Possell, H.I.J. Black, G. Kerstiens, R.D. Bardgett. 2004. Tree physiological responses to above-ground herbivory directly modify below-ground processes of soil carbon and nitrogen cycling. *Ecology Letters* **7**: 469 - 479
- Bazely, D.R., R.L. Jeffries. 1986. Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *Journal of Ecology* **74**: 693 – 706
- Bergerud, A.T., F. Manuel. 1968. Moose damage to balsam fir-white birch forests in central Newfoundland. *The Journal of Wildlife Management* **32(4)**: 729 – 746
- Borer, E.T., M.E.S. Bracken, E.W. Seabloom, J.E. Smith, J. Cebrian, E.E. Cleland, J.J. Elser, W.F. Fagan, D.S. Gruner, W.S. Harpole, H. Hillebrand, A.J. Kerkhoff, J.T. Ngai. 2013. Global biogeography of autotroph chemistry: is insolation a driving force? *Oikos* **122**: 1121 – 1130

- Bracken, M.E.S., H. Hillebrand, E.T. Borer, E.W. Seabloom, J. Cebrian, E.E. Cleland, J.J. Elser, D.S. Gruner, W.S. Harpole, J.T. Ngai, J.E. Smith. 2014. Signature of nutrient limitation and co-limitation: responses of autotroph internal nutrient concentrations to nitrogen and phosphorus additions. *Oikos* **124**: 113 – 121
- Brandner, T.A., R.O. Peterson, K.L. Risenhoover. 1990. Balsam fir on Isle Royale: Effects of moose herbivory and population density. *Ecology* **71(1)**: 155 - 164
- Bressette, J.W., H. Beck, V.B. Beauchamp. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. *Oikos* **121**: 1749 - 1760
- Bryant, J.P., F.S. Chapin III, D.R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* **40(3)**: 357 - 368
- Burney, O.T., D.F. Jacobs. 2013. Ungulate herbivory of boreal and temperate forest regeneration in relation to seedling mineral nutrition and secondary metabolites. *New Forests* **44**: 753 – 768
- Butler, L.G., K. Kielland. 2008. Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. *Journal of Ecology* **96**: 136 - 144
- Cebrian, J. 1999. Patterns in the fate of production in plant communities. *The American Naturalist* **154(4)**: 449 – 468
- Connor, K.J., W.B. Ballard, T. Dilworth, S. Mahoney, D. Anions. 2000. Changes in structure of a boreal forest community following intense herbivory by moose. *Alces* **36**: 111 – 132
- Côté, S.D., T.P. Rooney, J.P. Tremblay, C. Dussault, D.M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* **35**: 113 - 147

- Crête, M., C. Daigle. 1999. Management of indigenous North American deer at the end of the 20th century in relation to large predators and primary production. *Acta Veterinaria Hungarica* **47(1)**: 1 – 16
- DeGabriel, J.L., B.D. Moore, A.M. Felton, J.U. Ganzhorn, C. Stolter, I.R. Wallis, C.N. Johnson, W.J. Foley. 2014. Translating nutritional ecology from the laboratory to the field: milestones in linking plant chemistry to population regulation in mammalian browsers. *Oikos* **123**: 298 – 308
- De Jager, N.R., J. Pastor. 2009. Declines in moose population density at Isle Royale National Park, MI, USA and accompanied changes in landscape patterns. *Landscape Ecology* **24**: 1389 – 1403
- De Mazancourt, C., M. Loreau, L. Abbadie. 1999. Grazing optimization and nutrient cycling: Potential impact of large herbivores in a savanna system. *Ecological Applications* **9**: 784 – 797
- Dodds, D.G. 1983. Terrestrial mammals. Pp 509 – 550. G.R. South, ed. *Biogeography and Ecology of the Island of Newfoundland*. Dr. W. Junk Publishers: The Hague, Netherlands
- Ellis, R.C. 1960. Final report: An investigation of the length of regeneration period and of the yield potential of pulpwood cut-overs in Newfoundland. Department of Northern Affairs and National Resources Forestry Branch. Project NF 47. St. John's, Newfoundland
- Ellis, R.C., P.I. Pennington. 1988. Nitrification in soils of secondary vegetational successions from Eucalyptus forest and grassland to cool temperate rainforest in Tasmania. *Plant and Soil* **115**: 59 – 73

- Elser, J.J., R.W. Sterner, E. Gorokhova, W.F. Fagan, T.A. Markow, J.B. Cotner, J.F. Harrison, S.E. Hobbie, G.M. Odell, L.J. Weider. 2000a. Biological stoichiometry from genes to ecosystems. *Ecology Letters* **3**: 540 – 550
- Elser, J.J., W.F. Fagan, R.F. Denno, D.R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, S.S. Kilham, E. McCauley, K.L. Schulz, E.H. Siemann, R.W. Sterner. 2000b. Nutritional constraints in terrestrial and freshwater food webs. *Nature* **408(30)**: 578 – 580
- Frank, D.A. 2008. Ungulate and topographic control of nitrogen: phosphorus stoichiometry in a temperate grassland: soils, plants and mineralization rates. *Oikos* **117**: 591 - 601
- Fritz, H., A. Loison. 2006. Large herbivores across biomes. In K. Danell, R. Bergstrom, P. Duncan, and J. Pastor (Eds.) *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (19-49). Cambridge, UK: Cambridge University Press
- Gosse, J., L. Hermanutz, B. McLaren, P. Deering, T. Knight. 2011. Degradation of boreal forests by non-native herbivores in Newfoundland's National Parks: Recommendations for ecosystem restoration. *Natural Areas Journal* **31(4)**: 331 – 339
- Government of Canada. 2015. Newfoundland and Labrador – Weather Conditions and Forecast by Locations. <  
[https://weather.gc.ca/forecast/canada/index\\_e.html?id=NL](https://weather.gc.ca/forecast/canada/index_e.html?id=NL)>
- Harrison, K.A., R.D. Bardgett. 2004. Browsing by red deer negatively impacts on soil nitrogen availability in regenerating native forest. *Soil Biology & Biochemistry* **36**: 115 - 126

- Hessen, D.O., G.I. Ågren, T.R. Anderson, J.J. Elser, P.C. deRuitter. 2004. Carbon sequestration in ecosystems: the role of stoichiometry. *Ecology* **85**(5): 1179 – 1192
- Hester, A.J., M. Bergman, G.R. Iason, J. Moen. 2006. Impacts of large herbivores on plant community structure and dynamics. In K. Danell, R. Bergstrom, P. Duncan, and J. Pastor (Eds.) *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (97-141). Cambridge, UK: Cambridge University Press
- Hobbie, S.E. Effects of plant species on nutrient cycling. *TREE*. **7**(10): 336 – 339
- Joyce, T.L., S.P. Mahoney. 2001. Spatial and temporal distributions of moose-vehicle collisions in Newfoundland. *Wildlife Society Bulletin* **29**(1): 281 – 291
- Karns, P.D. 1998. Population distribution, density, and trends. P 134. A.W. Franzmann and C.C. Schwartz, eds. *Ecology and Management of the North American Moose*. Smithsonian Institution Press: Washington, D.C, United States of America
- Kielland, K., J.P. Bryant. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos* **82**(2): 377 – 383
- Leriche, H., X. LeRoux, J. Gignoux, A. Tuzet, H. Fritz, L. Abbadie, M. Loreau. 2001. Which functional processes control the short-term effect of grazing on net primary production in grasslands? *Oecologia* **129**: 114 – 124
- Martiny, A.C., C.T.A. Pham, F.W. Primeau, J.A. Vrugt, J.K. Moore, S.A. Levin, M.W. Lomas. 2013. Strong latitudinal patterns in the elemental ratios of marine plankton and organic matter. *Nature Geoscience Letters* DOI:10.1038/NGE01757
- McInnes, P.F., R.J. Naiman, J. Pastor, Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* **73**: 2059 – 2075



- McIntyre, P.B., A.S. Flecker. 2010. Ecological stoichiometry as an integrative framework in stream fish ecology. *American Fisheries Society Symposium* **73**: 000 - 000
- McLaren, B.E., S.P. Mahoney, T.S. Porter, S.M. Oosenbrug. 2000. Spatial and temporal patterns of use by moose of pre-commercially thinned, naturally-regenerating stands of balsam fir in central Newfoundland. *Forest Ecology and Management* **133**: 179 – 196
- McNaughton, S.J. 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. *The American Naturalist* **113**: 691 – 703
- Mikola, J., H. Setälä, P. Virkajärvi, K. Ilmarinen, W. Voigt, M. Vestberg. 2009. Defoliation and patchy nutrient return drive grazing effects on plant and soil properties in a dairy cow pasture. *Ecological Monographs* **79(2)**: 221 – 244
- Newfoundland and Labrador Environment and Conservation. 2014. 2014-2015 Hunting and Trapping Guide.  
<<http://www.env.gov.nl.ca/env/wildlife/pdf/HuntingGuide2014-15lowres.pdf>>
- Niwa, S., L. Mariani, N. Kaneko, H. Okada, K. Sakamoto. 2011. Early-stage impacts of sika deer on structure and function of soil microbial food webs in temperate forest: A large scale experiment. *Forest Ecology and Management* **261**: 391 – 399
- Olofsson, J., L. Oksanen. 2002. Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: A litterbag experiment. *Oikos* **96(3)**: 507 - 515
- Parks Canada. 2013. Forest Health in Terra Nova National Park. <<http://www.pc.gc.ca/eng/progs/np-pn/sf-fh/terranova/lgde-sm.aspx>>

- Pastor, J., R.J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. *The American Naturalist* **139(4)**: 690 – 705
- Pastor, J., R.J. Naiman, B. Dewey, P. McInnes. 1988. Moose, microbes, and the boreal forest. *BioScience* **38(11)**: 770 - 777
- Pimlott, D.H. 1953. Newfoundland moose. *Transactions of the North American Wildlife Conference* **18**: 563 – 581
- Pimlott, D.H. 1959. Reproduction and productivity of Newfoundland moose. *Journal of Wildlife Management* **23**: 381 – 401
- Rae, L.F., D.M. Whitaker, I.G. Warkentin. 2013. Multiscale impacts of forest degradation through browsing by hyperabundant moose (*Alces alces*) on songbird assemblages. *Diversity and Distributions* DOI: 10.1111/ddi.12133
- Ritchie, M.E., D. Tilman, J.M.H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* **79(1)**: 165 – 177
- Rogerson, R.J. 1983. Geological evolution. Pp. 5 – 35. G.R. South, ed. *Biogeography and Ecology of the Island of Newfoundland*. Dr. W. Junk Publishers: The Hague, Netherlands
- Rossow, L.J., J.P. Bryant, K. Kielland. 1997. Effects of above-ground browsing by mammals on mycorrhizal infection in an early successional taiga ecosystem. *Oecologia* **110**: 94 – 98
- Schmitz, O.J., D. Hawlena, G.C. Trussell. 2010. Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13(10)**: 1199 – 1209
- Sterner, R.W., J.J. Elser. 2002. *Ecological Stoichiometry: The Biology of Elements from Molecules to Biosphere*. Princeton, New Jersey: Princeton University Press

- Stone, E.L., W.T. Swank, J.W. Hornbeck. 1979. Impacts of timber harvest and regeneration on stream flow and soils in the eastern deciduous region in C.T. Youngberg (ed). *Forest Soils and Land Use*. Colorado State University Press: Fort Collins
- Strong, J.S., S.J. Leroux. 2014. Impact of non-native terrestrial mammals on the structure of the terrestrial mammal food web of Newfoundland, Canada. PLoS ONE DOI: 10.1371/journal.pone.0106264
- Tabuchi, K., D.T. Quiring, L.E. Flaherty, L.L. Pinault, K. Ozaki. 2011. Bottom-up trophic cascades caused by moose browsing on a natural enemy of galling insect on balsam fir. *Basic and Applied Ecology* **12**: 523 – 531
- Thompson, I.D., A.U. Mallik. 1989. Moose browsing and allelopathic effects of *Kalmia angustifolia* on balsam fir regeneration in central Newfoundland. *Canadian Journal of Forest Research* **19**: 524 – 526
- Thompson, I.D., W.J. Chapin. 1993. A re-examination of moose damage to balsam fir-white birch forests in central Newfoundland: 27 years later. *Canadian Journal of Forest Research* **23**: 1388 – 1395
- Thompson, I.D., W.J. Curran, J.A. Hancock, C.E. Butler. 1992. Influence of moose browsing on successional forest growth on black spruce sites in Newfoundland. *Forest Ecology and Management* **47**: 29 – 37
- van Cleve, K., F.S. Chapin III, C.T. Dyrness, L.A. Viereck. 1991. Element cycling in taiga forests: State-factor control. *BioScience* **41(2)**: 78 - 88

- Wardle, D.A., G.M. Barker, G.W. Yeates, K.I. Bonner, A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forest: aboveground and belowground consequences. *Ecological Monographs* **71(4)**: 587 – 614
- Wardle, D.A., K.I. Bonner, G.M. Barker. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology* **16(5)**: 585 – 595
- Wardle, D.A., R.D. Bardgett. 2004. Human-induced changes in large herbivorous mammal density: The consequences for decomposers. *Frontiers in Ecology and the Environment* **2(3)**: 145 – 15

**Table 1. 1:** Summary of grazer and browser effects in a variety of ecosystems found globally.

Feeding preference	Species	Location	Summary of effects	Reference
Grazers	Wildebeests ( <i>Connochaetes taurinus</i> )	Serengeti, Africa	Grassland productivity increased under moderate grazing intensity	McNaughton 1979
	Impala ( <i>Aepyceros melampus</i> ), zebra ( <i>Equus burchellii</i> ), waterbuck ( <i>Kobus ellipsiprymus</i> ), buffalo ( <i>Sycerus caffer</i> ), eland ( <i>Taurotragus oryx</i> )	Kenya, Africa	Grazing stimulated aboveground plant production by 22% in nutrient rich glade sites and reduced it by 68% at nutrient poor bushland sites	Sankaran and Augustine 2004
	Bison ( <i>Bison bison</i> ), elk ( <i>Cervus elaphus</i> ), and pronghorn ( <i>Antilocapra americana</i> )	Yellowstone National Park, USA	Grazing enhanced plant N concentrations	Frank 2008
	Dairy cow	Maaninka, Finland	Grazing increased shoot P and N by 65% and 33% respectively	Mikola et al. 2009.
	Lesser snow geese ( <i>Anser caerulescens caerulescens</i> )	Manitoba, Canada	Grazing promoted growth of <i>Carex</i> and <i>Puccinellia</i> , while removal of grazer promoted growth of <i>Potentilla egedii</i>	Bazely and Jeffries 1986
Browsers	Moose ( <i>Alces alces</i> )	Isle Royale, Lake Superior, USA	Browsing prevented growth of preferred plants and shifted plant communities from balsam fir ( <i>Abies balsamea</i> ) dominant to white spruce ( <i>Picea glauca</i> ) dominant	McInnes et al. 1992
	White tailed deer ( <i>Odocoileus virginianus</i> )	Virginia, USA	Browsing reduced the amount of leaf litter and vegetation cover, and altered plant species composition	Bressette et al. 2012
	Moose ( <i>Alces alces</i> )	Alaska, USA	Reduced biomass of willow in areas of high moose density and	Butler and Kielland 2008

			higher mortality rates under increased browsing pressure	
	Goat ( <i>Capra hircus</i> ) and deer ( <i>Cervus elaphus scoticus</i> )	New Zealand	Browsing by introduced species reduced preferred species and accelerated the growth of less palatable plants.	Wardle et al. 2001
	Sika deer ( <i>Cervus nippon</i> )	Ibaraki Prefecture, Japan	3 years after introduction of browser to enclosure, understory cover of dwarf bamboo ( <i>Sasa nipponica</i> ) declined	Niwa et al. 2011

## **1.6. Co-Authorship Statement**

Chapter 2 is under submission for publication and is co-authored by Dr. Shawn Leroux. As such, there will be necessary repetition between Chapters 1, 2, and 3. I was responsible for project development, design, field sampling, laboratory work, analysis, and writing, and my co-author guided all aspects of this project.

## **CHAPTER 2: Introduced moose directly impact plant regeneration but have limited indirect effects on soil stoichiometry and litter decomposition rates in Newfoundland, Canada**

### **2.1. Introduction**

Recent accumulation of theoretical and empirical evidence shows that consumer species can store large quantities of nutrients in their bodies (Vanni 2002) and they can influence ecosystem nutrient cycling through a number of consumptive and non-consumptive mechanisms (Leroux & Loreau 2010; Schmitz et al. 2010). Ecological stoichiometry can help elucidate the effects of consumers on ecosystems by predicting the chemical needs of species across trophic levels (Elser et al. 2000). Herbivores are an important component of consumer biota as herbivores can determine the distribution of elements among trophic levels within ecosystems as well as determine the chemical content of organic matter substrates on which microbes ultimately act (Leroux & Schmitz 2015). Specifically, herbivores can directly and indirectly modify both the structure and function of ecosystems by selectively consuming plant material and thereby indirectly altering soil and litter quantity and quality (Hobbs 1996; Wardle et al. 2002; Bardgett & Wardle 2003) as well as inducing plant chemical defences (Bardgett et al. 1998; Bardgett and Wardle 2003). In this study, I seek to explain if an introduced herbivore species alters nutrient cycling in previously disturbed forest ecosystems.

Herbivores can physically modify the structure and function of ecosystems; for example, dam building by beavers (*Caster canadensis*) cause large ecosystem changes through the impoundment of streams and marshes (Naiman et al. 1988). Herbivory



removes plant tissue and reproductive material that directly affect plant productivity (Hester et al. 2006). The return of material through deposition of excreta and carcasses creates localized areas of labile nitrogen concentration, enhancing nutrient availability to soil ecosystems, and increasing nutrient uptake by plants (Pastor et al. 1988; Molvar et al. 1993; Steinauer and Collins 1995; Hobbs 1996; Fornara & Du Toit 2008; Bump et al. 2009; Murray et al. 2013). For example, graminoid and forb production increased one year after bovine urine treatment was applied in Kansas and Nebraska (Steinauer & Collins 1995). As herbivores move through their range, they deposit nutrients in small localized patches (Hobbs 1996) increasing quantity and quality of nutrient inputs to the soil. However, excreta hotspots may not compensate for long term or broad scale changes in litter quality and quantity (Pastor et al. 1993; Steinauer & Collins 1995).

The indirect effects of herbivores can influence ecosystems over much larger spatial and temporal scales than their direct effects of removal of plants and return of excreta (Pastor et al. 1993; Pastor et al. 1998; Olofsson & Oksanen 2002) and there continues to be a large body of research focused on deciphering indirect effects of herbivore consumers (see review Rooney & Waller 2003; Côté et al. 2014). Herbivores can facilitate feedbacks between plants and soil ecosystems, resulting in deceleration or acceleration of succession depending on feeding preferences of grazers or browsers respectively. For example, browsers, such as white tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*), consume nutrient rich woody species (low C:N:P) resulting in a community shift towards poor quality (high C:N:P) plant material (Brandner et al. 1990; van Cleve et al. 1991; Rossow et al. 1997; DeJager & Pastor 2009). Conversely, grazing can stimulate dominance of preferred plant species through increased nutrient uptake,

faster growth rates in remaining plant components, and higher tissue nutrient concentration (Leriche et al. 2001)

The mechanisms by which herbivores can modify communities directly result in trophic cascades on ecosystem structure and function (see review by Wardle et al. 2004). Trophic cascades occur when changes in the biomass or abundance of one trophic level of the ecosystem results in changes in the biomass or abundance of non-adjacent trophic levels of the ecosystem (Pace 1999; Polis 1999; Bressette et al. 2012). The indirect effects of herbivores on ecosystems modify aboveground and belowground mechanisms (Rossow et al. 1997; Wardle et al. 2004; Nuttle et al. 2011; Bressette et al. 2012), influencing nutrient cycling (Carline et al. 2005), tree regeneration (Gosse et al. 2011), and populations of invertebrates (Teichman et al. 2013), birds (Rae et al. 2013), and other species.

Moose have a number of direct and indirect effects on the boreal ecosystems they inhabit. Weighing approximately 360 kilograms, moose consume red maple, white birch, trembling aspen, balsam fir, and other woody species and it has been estimated that one individual can eat between 3000 to 5000 kilograms of dry matter per year (Pastor et al. 1993). Under varying moose densities, forest composition changes and climax species prevail. For example, on Isle Royale, USA, moose presence resulted in a change from hardwood and balsam fir dominant sites to black spruce dominant savannahs (Brandner et al. 1990; Risenhoover & Maass 1987; McInnes et al. 1992; DeJager & Pastor 2009). In Alaska, the age class of willow is young, and the density of later successional species of alder (*Alnus tenuifolia*) and poplar (*Populus balsamifera*) has increased under high moose densities (van Cleve et al. 1991; Rossow et al. 1997; Butler & Kielland 2007). Our

knowledge of moose effects on boreal ecosystems is based on a select few long-term studies based in Isle Royale and Alaska. Here I aim to determine if the patterns of moose effects on forest ecosystems observed in Isle Royale and Alaska play out in Newfoundland, Canada; an ecosystem with different environmental conditions (e.g. marine island environment surrounded by salt water) in disturbed forests in which moose were introduced.

Two moose were introduced to Newfoundland in 1878 and four more were introduced in 1904 (Pimlott 1953). Since then the population has grown to the highest density (0.41 - 7 moose/km<sup>2</sup> (Joyce & Mahoney 2001)) in the world. In 2014 the population of moose was around 112,000 individuals excluding those found in National Parks (Newfoundland and Labrador Wildlife Division 2015) with approximately 194 individuals in TNNP. The large introduced moose population is of concern in Newfoundland as moose have no natural predators on the island, and their population is only controlled through hunting. Forest regeneration, following logging and other disturbances, is being negatively affected by the high moose population (Ellis 1960; Gosse et al. 2011). For example, Connor et al. (2000) found species diversity declined as moose populations increased over a 20 year period in GMNP. While moose effects on forest regeneration and nutrient cycling has been intensively studied in other boreal forest systems (see Risenhoover & Maas 1987; Brandner et al. 1990; McInnes et al. 1992; Pastor et al. 1993; Rossow et al. 1997; Pastor et al. 1998; Butler & Kielland 2007; DeJager & Pastor 2009), research in Newfoundland has primarily focused on forest regeneration (Ellis 1960; Thompson et al. 1992; Thompson and Curran 1993; Gosse et al. 2011; Humber & Hermanutz 2011). The purpose of our study is to examine the short term

(18-20 year) effects of moose on nutrient cycles in previously disturbed ecosystems of Newfoundland, Canada. Using established 15-20 year old moose exclosures, I aimed to test the following predictions:

- a) in areas that are heavily browsed by moose, the plant community will shift to less palatable spruce-moose savannah (Ellis 1960; McInnes et al. 1992; Pastor et al. 1993; McLaren et al. 2009);
- b) in areas that are heavily browsed by moose, the quantity and quality of litter will be lower (i.e. higher C: N ratio) than that in areas of exclosure (Pastor et al. 1993; Pastor et al. 1998);
- c) in areas that are heavily browsed by moose, the quality of soil will be lower (i.e. higher C: N ratio) than that in areas of moose exclosures (Pastor et al. 1993; Pastor et al. 1998); and
- d) in areas that are heavily browsed by moose, litter decomposition will be slower than in areas of exclosure (Stark et al. 2000; Yates et al. 2000; Sankaran & Augustine 2004; Sørensen et al. 2009; Haynes et al. 2014) (Table A.1).

## **2.2. Study area**

I conducted my study in the Central Newfoundland Forest ecoregion, North Shore forest ecoregion, and the Avalon Forest ecoregion of the island of Newfoundland, Canada. In the Central Newfoundland Forest ecoregion, I had five sites in Terra Nova National Park (TNNP) and three sites near Clarenville, Newfoundland (Figure 2.1). The Central Newfoundland forest ecoregion experiences some disturbance from fire and insects,

resulting in black spruce (*Picea mariana*) dominant forests, mixed with stands of balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*) (Bell 2002). TNNP overlaps with the North Shore Forest Ecoregion. Similar to the Central Newfoundland Forest ecoregion, the North Shore Forest ecoregion is characterized by stands of balsam fir, white spruce, and trembling aspen (Bell 2002). TNNP had a moose density of 0.59 moose·km<sup>2</sup> while the moose management area encompassing Clarenville had a moose density of 2.47 moose·km<sup>2</sup> (Joyce & Mahoney 2001).

Our two sites in the Avalon Forest ecoregion were dominated by balsam fir, white and yellow birch (*Betula alleghaniensis*) (Bell 2002). The moose management area encompassing the two Avalon sites had a moose density of 3.57 moose·km<sup>2</sup> (Joyce & Mahoney 2001).

### **2.3. Methods**

I used moose exclosures, fenced areas that exclude moose, to compare areas without (inside exclosure) and with (adjacent reference sites) moose herbivory. The exclosures I used were established in forests previously disturbed prior to exclosure installation. The exclosures effectively exclude moose but small herbivores, such as snowshoe hare (*Lepus americanus*), are able to access plant material within the exclosure. I used 10 previously established paired moose exclosures and references (Table 2.1) to examine moose effects (Blue Hill centre, edge and west, Ochre Hill, Platter's Cove, Fox Marsh 1 and 2, Port Blandford centre and edge, and Thorburn Lake). I classified the exclosure/reference pair into five different disturbance regimes based on previous disturbances, dominant tree

type, and location. The five exclosures in TNNP and the three exclosures in the Clarendville area (Figure 2.1) were approximately 2.5 m high fences that were 35 m x 35 m. On the inside edge of each exclosure there was a 5 m buffer to minimize the impacts of moose browse adjacent to the exclosure. I placed four 4m x 4m plots in one corner of the established exclosures due to other established plots in the centre of each exclosure (Figure A.1A). Each exclosure was paired with an adjacent reference of the same size; plots within the reference sites were also 4 m x 4 m, following the same layout as the exclosure. The paired exclosure/reference plots in TNNP and around Clarendville fell in four different disturbance regimes: insect infestation from the 1970's (Blue Hill centre and edge); insect infestation from the 1970's in a spruce dominant stand (Blue Hill West); insect infestation from the 1970's as well as disturbance from Hurricane Igor in 2010 (Ochre Hill and Platter's Cove); and a balsam fir stand cut in 1995 (Port Blandford centre and edge, and Thorburn Lake) (Table 2.1).

The two exclosures on the Avalon Peninsula were 15 m x 15 m with a 2 m buffer on each edge. To maintain four 4 m x 4 m plots, two plots were allocated to opposite corners of the exclosures as previously established plots ran through the centre of the exclosure (Figure A.1B). Four 4 m x 4 m reference plots were delineated to be consistent with the exclosure plots on the Avalon Peninsula. The Avalon Peninsula sites (Fox Marsh 1 and 2) (Figure 2.1) were classified in their own disturbance regime based on location as they were established in a balsam fir stand logged in 1995 (Table 2.1).

### *2.3.2 Field and Laboratory Methods*

#### *a. Plant community composition*

To measure plant composition in exclosure and reference areas, I divided each 4 m x 4 m plot into four 2 m x 2 m subplots (Figure A.1) and then randomly selected one subplot for plant identification. I identified all plant species within this subplot using *Plants of the Western Forest* (Johnson et al. 1995) and *Trees and Shrubs: Newfoundland and Labrador* (Boland 2013). I measured the height and basal diameter of all shrubs and trees between 30 cm and 200 cm tall, and estimated the height of all shrubs and trees above 200 cm tall. I also noted if a shrub or tree was browsed by moose, hare or both. I used 30 cm as the cut off as winter browse is typically above this height due to snowpack. I identified and estimated the percent cover of all plants under 30 cm in height, along with herbs, grasses and ferns.

I tested four specific predictions from our general plant composition prediction (see prediction a) to determine how plant species might be affected by moose presence or absence:

- a.1) moose exclosures will be more diverse than reference areas (Risenhoover & Maas 1987; Rooney & Waller 2003; Mathisen et al. 2010);
- a.2) moose exclosures will have more preferred species than reference areas and have the same number of non-preferred species (McInnes et al. 1992; Rooney & Waller 2003; Mathisen et al. 2010; Gosse et al. 2011; Bachand et al. 2014);
- a.3) moose exclosures will have more preferred individuals than reference areas and have the same number of non-preferred individuals (Risenhoover & Maas 1987; Thompson & Mallik 1988; McInnes et al. 1992; Thompson &

Curran 1993; Wardle et al. 2001; Rooney and Waller 2003; Tabuchi et al. 2011); and

a.4) moose exclosures will have taller preferred individuals than references while the height of non-preferred individuals does not differ between exclosures and control plots (Ellis 1960; Bergerud & Manuel 1968; Brandner et al. 1990; Kielland & Bryant 1998; Edenuius et al. 2001; Gosse et al. 2011).

I assigned preference based on previous studies in Newfoundland (Pimlott 1955; Dodds 1960; Tanner & Leroux 2015). Species not assigned as preferred in these papers were assumed to be non-preferred species (Table A.2).

*b. Plant litter fall quantity and quality*

I placed four 36 cm tall by 660.5 cm<sup>2</sup> cylindrical plastic litter fall traps on August 1-12, 2014 in each exclosure/reference pair and checked them monthly (Table A.3). After three months, on November 8 - 9 2014, I collected all plant litter material within each trap and placed it in a plastic bag. I discarded branches larger than one cm in diameter at the site. I removed two traps from our analysis as I found animal remains in them (Blue Hill west control and Port Blandford centre control). Litter was stored in a freezer at -20°C for two months until it could be processed in the laboratory.

In the lab, I air-dried the plant litter biomass of each litter trap for 48 hours on aluminium trays. I sorted the air-dried material into leaves and needles by species, wood, and seeds and cones. I weighed the sorted contents of each trap before oven drying the samples at 50°C until constant weight (~48 hrs). I ground the oven-dried material of each sample by hand using a mortar and pestle.



To measure litter quality, I sent each sample for analysis of % carbon (C), % nitrogen (N), % phosphorus (P) as well as determination of ppm for potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), copper (Cu), manganese (Mn), zinc (Zn), and boron (B) to the Soil, Plant and Feed Laboratory, at the Newfoundland & Labrador Department of Natural Resources. For most species, however, I had very little plant litter biomass. Consequently, I combined samples from all moose exclosure/reference sites to get one homogenized litter sample per species to have sufficient sample for chemical analysis. For four species (balsam fir, white birch, red maple, and black spruce) I had sufficient material to test for elemental differences between moose exclosures and reference areas as well as measure the homogenized elemental composition of the litter (Table A.4). Carbon and N were analyzed on a Combustion Analyzer (LECO CNS 2000) using a version of AOAC method 990.03 (Combustion Method). The remaining nine elements were analyzed following a version of AOAC method 985.01 (Inductively Coupled Plasma Spectroscopic Method) and read on ICP (Prodigy High Dispersion ICP – Teledyne Leeman Labs). I present the results for C, N, and P here and patterns for the remaining elements in an appendix (Figure A.2).

I had two specific predictions within our litter fall quality and quantity predictions (see prediction b) by which plant litter fall could vary between moose exclosures and references:

- b.1) the biomass of litter falling would be greater in exclosures than references; and
- b.2) the molar mass of nutrients (C, N, P) and nutrient ratios (C:N, N:P) in plant litter traps would be greater in exclosures than references.

*c. Soil nutrient quality*

In order to test prediction c) I collected four soil cores to a maximum depth of 30 cm using an Eijkelkamp One-Piece Edelman Auger® on August 1-12, 2014 from each plot. I combined subplot soil cores and layers to form one bulked soil sample per plot. I measured the depth of each soil core and averaged depth across the plot. I stored samples in plastic bags, transported in a cooler, and kept at approximately 4°C in a refrigerator for two months until I began processing in the laboratory.

Once in the lab, I sieved each soil sample through a 1.5 mm screen to remove macro-invertebrates, woody debris, stones, roots, and moss, and homogenized the remaining material by hand. Where there was at least 5 g of soil, I made a slurry with distilled water and measured the pH of the soil using the Accumet® 15/15+ bench top meter. I dried  $20 \pm 0.1$  g of homogenized sample in a drying oven at 80°C until constant weight (~48 hrs). I calculated percent moisture of the soil samples as the difference between [(wet weight and oven dry weight)/wet weight]. I ground the oven dried soil to a fine powder. I sent approximately 5 g of each sample for analysis of % C, % N, as well as determination of the concentration (ppm) for P, K, Ca, Mg, Fe, Cu, Mn, Zn, and B to the Soil, Plant and Feed Laboratory as part of the Newfoundland & Labrador Department of Natural Resources. I converted the concentration of P in each homogenized soil sample to % by dividing ppm by 10,000. I present the results for soil % C, N, and P here and patterns for the remaining elements in the appendix (Figure A.3).

*d. Litter decomposition*

To test prediction d) I collected leaves of white birch and needles of balsam fir in July 2014 from one canopy in Pippy Park, Newfoundland (47.575005, -52.742688). I placed 1

g of air dried (~48 h) white birch and 1 g of air dried balsam fir in 15cm x 15cm black 1 mm nylon mesh bags. Each bag was cinched with yellow nylon rope and stored in paper bags in a cooler up to two weeks until they were deposited at each site.

In each plot within each paired enclosure/control area, I placed three decomposition bags, for a total of 240 bags, from August 1-12, 2014. I staked decomposition bags with a florescent flag for easy relocation. I collected one bag from each plot after approximately one, two and three months, with the last bags being collected in November 2014 (Table A.3) and stored at 4°C in a refrigerator before being processed in the laboratory immediately following collection. Seven bags were lost through herbivory or trampling and were not included in the data set (Table A.4).

In the lab, I randomly selected each bag, and carefully emptied and rinsed the contents with distilled water through a 1 mm sieve to remove macroinvertebrates. I weighed the wet material and the contents were placed in a drying oven at 50°C until constant weight (~48 hrs). I ground samples using a mortar and pestle, and ashed subsamples in a muffle furnace for 4 hours at 500°C to obtain ash free dry mass (AFDM). Eleven samples were spilled in the muffle furnace and were subsequently removed from the AFDM data set (Table A.4).

### *2.3.3 Modelling approach*

In all models for a) plant community composition, b) litter fall quantity and quality, and c) soil quality I included one fixed effect, enclosure/reference; and two random effects, site nested in disturbance regime. The general model formula was:

Response variable ~ enclosure/reference + (site nested in disturbance regime)

I used site (10 levels) as a random variable because our enclosure and reference areas were paired by site. I included disturbance regime (five levels) as a random variable because multiple sites fell within the same disturbance regime and I expected disturbance to explain some of the variation in plant composition. I used a model with only the random intercept of site nested in disturbance regime as a null model to ascertain if adding additional fixed effects (e.g. moose enclosure/reference) improves model fit relative to a model with only the random intercepts of site nested in disturbance regime. I tested the assumptions for normal distribution of the residuals and where they were not normally distributed, I natural log transformed the response variable (litter biomass; molar mass C, N, P). I used Akaike Information Criterion, corrected for small sample size ( $AIC_c$ ), to determine the weight of evidence in support of an effect of moose presence on plant composition, litter quantity and quality, soil quality, and decomposition rate. If a model with moose enclosure/control had a lower  $AIC_c$  ( $<2$ ) than our null model, I considered this evidence in support of our fixed effect of moose presence/absence as an important predictor of plant composition, litter quantity and quality, soil quality, and decomposition rate. I performed all statistical analyses using the lmer function within the lme4 package (Bates and Mäechler 2015) in R. v.3.1.2 (R Core Team 2013).

*a. Plant community composition*

In order to test prediction a.1) I used linear mixed models to test for differences in plant species diversity between moose enclosures and references using the Shannon Wiener and Simpson species diversity indices as our response variable. I used the Shannon Wiener and Simpson function within the vegan package (Oksanen, et al. 2015) in R v.3.0.1 (R Core Team 2013) to obtain the diversity index for each site.

In order to test predictions a.2 & a.3) I fit linear mixed models to test for differences in the number of preferred and non-preferred species and individuals between moose exclosures and references. Our response variable was the total number of preferred or non-preferred species or individuals per exclosure or reference area.

In order to test prediction a.4) I fit linear mixed effects models to test for the differences in the height of preferred (and non-preferred) species between moose exclosures and references. Height was a continuous variable between 30 cm and 200 cm.

In addition to our general linear mixed effects model, I performed a nonmetric multidimensional scaling method (NMDS) to observe how surveyed tree and shrub species were distributed across our treatments (moose exclosure/reference), study sites and disturbance regimes using the “metaMDS” function in the vegan package (Oksanen et al. 2015) in R v.3.1.2 (R Core Team 2013). I used Bray-Curtis distance measures to calculate the distances between species composition and abundance across our sites. I used a two dimensional solution as this achieved the lowest global stress value (0.1546) explaining plant species composition and abundance.

I computed the correlations between species scores and each NMDS axes using the Pearson’s Product-Moment correlation (r-value). I considered a species to be significantly correlated to one of the NMDS axes if they had a r-value  $|r| > 0.423$  ( $n=20$ ,  $p < 0.05$ ; Upton and Cook 2008). I added a second matrix of environmental variables including: five environmental factors (soil pH, soil moisture, canopy cover, % woody debris cover, and slope) and three categorical location variables (exclosure/reference, site and disturbance regime) to determine their association with species composition and

abundance. I fit this matrix to our species ordination using the “envfit” function in the vegan package.

*b. Plant litter fall quantity and quality*

I used linear mixed models to test for differences in the total plant litter quantity between moose exclosures and references using litter biomass (prediction b.1), and molar mass of C, N, and P (prediction b.2) as our response variables. My data suggest that there are only small differences in % C, % N, and % P of balsam fir, red maple, white birch, and black spruce between moose exclosure, control and homogenized samples (Table A.5).

Specifically, the mean difference in balsam fir % C, % N, and % P between moose exclosure and control was 1.59 %, 0.026 %, and  $3.96e^{-2}$  %, respectively. Consequently, I used % C, % N, and % P homogenized litter samples as the response variable for the remainder of our analysis. I converted % C, % N, and % P to moles for each species when there was adequate material present in a sample (Table A.6). I summed the values across moose exclosure and controls to obtain total molar mass of C, N, and P for every site. I calculated the molar ratios of C:N and N:P using the summed molar masses for each site.

*c. Soil nutrient quality*

I used linear mixed models to test for differences in the quality of soil between moose exclosures and controls using percent C, N, and P as our response variables (prediction c). Phosphorus was analyzed as ppm, and I transformed it into percentage for analyses. I added three additional fixed effects (soil pH, soil moisture, and soil depth) to our basic model to test for differences in soil quality to see if the effects explained some of the variation in soil quality between moose exclosures and controls. I looked for correlations between our fixed and random variables and found no correlations between them.

#### *d. Litter decomposition*

I used linear mixed models to test for differences in litter decomposition between moose exclosures and references (prediction d). I fit linearized negative exponential decay models (ie.  $M_t = M_0 e^{-kt}$  transformed to  $\ln(M_t) = \ln(M_0) - kt$ ) with natural ln transformed oven dry mass as our response variable. To test for differences in litter decomposition (d), I included four fixed effects including the two-way interaction term: time, moose exclosure/reference, time\*moose exclosure/reference, soil moisture, and soil depth. I included soil characteristics as these abiotic conditions are important predictors of litter decomposition (Mayer 2008). I had included soil pH in our initial candidate model set but found it to be a pretending variable and therefore it was removed as an explanatory variable. I also included two random effects: site nested in disturbance regime in my model.

## **2.4. Results**

#### *a. Plant community composition*

I observed a qualitative concordance between our Shannon-Wiener (H) and Simpson (D) indices (Table A.7) and therefore present the results for Shannon-Wiener here and Simpson diversity in the appendix (Table A.8). Contrary to our hypothesis a.1), I did not find evidence for a difference in plant species diversity between moose exclosures and references (Figure 2.2A & Table 2.2). Blue Hill centre was the most diverse exclosure (median H = 1.89) and Fox Marsh 2 was the least diverse exclosure (median H = 0.18). Thorburn Lake was the most diverse reference (median H = 2.19) and Fox Marsh 2 was the least diverse reference (median H = 0.14). The greatest difference in diversity

between exclosure and reference occurred in Platter's Cove with the exclosure (median  $H = 1.52$ ) being more diverse than the reference (median  $H = 0.68$ ). Most of the variation in species diversity among sites was explained by disturbance regime and site (conditional  $R^2 = 0.645$ ; Table 2.2).

The model with the term moose exclosure/reference did not improve model fit for the number of preferred (marginal  $R^2 = 0.0$ ,  $\Delta AIC_c = 2.87$ ) and non-preferred (marginal  $R^2 = 0.004$ ,  $\Delta AIC_c = 3.94$ ) species. Overall, my sites had fewer non-preferred than-preferred plant species (Figure 2.2B). The median ( $\pm$  sd) number of preferred species in exclosure and reference was  $3.5 (\pm 1.71)$  and  $2.5 (\pm 2.11)$ , respectively. Blue Hill edge control had the most preferred species ( $n=8$ ) while the exclosures with the most preferred species were Blue Hill centre and edge ( $n=6$ ). The median number of non-preferred species in exclosure and reference was  $3 (\pm 0.78)$  and  $3 (\pm 1)$  respectively. Ochre Hill reference had the most non-preferred species ( $n=5$ ) while the exclosure with the most non-preferred species were Blue Hill edge and Blue Hill west ( $n=4$ ). Fox Marsh 2 did not have any non-preferred species in either exclosure or reference.

A model that included moose exclosure/reference had a lower  $\Delta AIC_c$  than the null model providing weak evidence that moose presence or absence had an effect on the number of preferred (marginal  $R^2 = 0.0009$ ,  $\Delta AIC_c = 0$ ) and non-preferred (marginal  $R^2 = 0.1335$ ,  $\Delta AIC_c = 0$ ) individuals (Table 2.2). There were  $35.2 (\pm 20.99)$  preferred individuals in exclosures and  $36.9 (\pm 35.59)$  preferred individuals in references (Figure 2.2C). Fox Marsh 2 reference had the greatest number of preferred individuals ( $n=126$ ) while Blue Hill West exclosure had the least number of preferred individuals ( $n=7$ ). There were fewer non-preferred individuals in exclosures ( $32.78 \pm 19.90$ ) than in references



(67.89  $\pm$  61.00). Ochre Hill reference had the greatest number of non-preferred individuals (n=188) while Blue Hill centre exclosure had the fewest number of non-preferred individuals (n=5).

As with species diversity, disturbance regime and site explained a lot of the variation in the number of preferred and non-preferred species (conditional  $R^2 = 0.59$  and  $0.21$ , respectively) and individuals (conditional  $R^2 = 0.23$  and  $0.30$ , respectively) among sites (Table 2.2).

I found evidence that evidence that moose presence or absence explained some of the observed differences in height of preferred individuals ( $\Delta AIC_c = 0$ ) and non-preferred plant individuals ( $\Delta AIC_c = 0$ ) (Table 2.2). Preferred plant individuals had a median ( $\pm$  sd) height of 98 ( $\pm$  56.93) cm and 58.1 ( $\pm$  50.23) cm in exclosures and references, respectively (Figure 2.2D). The largest difference in preferred plant height between exclosure and reference occurred at Thorburn Lake with a difference in median height of 68.08 cm. The median ( $\pm$  sd) height of non-preferred individuals in exclosures and references was 73.5 ( $\pm$  35.76) cm and 57.3 ( $\pm$  24.73) cm respectively. The largest difference in non-preferred plant height between exclosure and reference occurred at Thorburn Lake with a difference in median height of 68.14 cm. The fixed effect of moose exclosure and reference explained 13.15% of the variance in height of preferred individuals and 8.55% of the variance in height of non-preferred plant individuals among sites (Table 2.2) with taller individuals being found in moose exclosures (Table A.9). As above, I found evidence that disturbance regime and site explained some of the variance in preferred and non-preferred plant height among sites.

In total, I observed 24 tree and shrub species in 10 paired enclosure/reference locations. Eight plant species (balsam fir, Labrador tea, mountain maple, red maple, service berry, sheep laurel, swamp red currant, wild raspberry) were significantly correlated with either NMDS axis 1 or NMDS axis 2 (Figure 2.3). Soil pH was the only environmental variable that was significantly correlated with either axis (NMDS axis 2,  $R^2 = 0.4688$ ,  $p > 0.001$ ). Enclosure and reference was not significantly correlated with any axes in our NMDS, however, both disturbance ( $R^2 = 0.5071$ ,  $p > 0.001$ ) and site ( $R^2 = 0.7958$ ,  $p > 0.001$ ) were correlated with either NMDS axis 1 or NMDS axis 2.

*b. Plant litter quantity and quality*

Inclusion of a term for moose enclosure/reference led to a large improvement in the fit of our model to explain variation in litter biomass ( $\Delta AIC_c = 0$ ) suggesting that moose presence/absence influenced variation in the amount of plant litter biomass in autumn 2014. The fixed effect of moose enclosure and reference explained 45.06% of the variance in the natural log biomass of plant litter among sites (Table 2.3). Litter traps in moose exclosures had a median ( $\pm$  sd) litter biomass of 29.36 ( $\pm$  15.73) g of litter after four months and references had a median ( $\pm$  sd) of 4.19 ( $\pm$  20.42) g of plant litter biomass (Figure 2.4D). Litter mass ranged from 62.57 g (Fox Marsh 2) to 16.69 g (Blue Hill West) in exclosures and 58.65 g (Platter's Cove) to 0.80 g (Port Blandford centre) in references. The greatest difference in litter biomass between paired enclosure/reference sites were observed in Thorburn Lake (52.31 g more in enclosure) and Platter's Cove (9.31 g more in reference). The conditional  $R^2$  of our top model was 0.66, suggesting that disturbance regime and site also explained some of the variation in natural log biomass of plant litter among sites.

Inclusion of the term moose enclosure/reference improved the fit our model to explain variation in the quantity of available C, N, and P (Table A.10). Specifically, moose enclosure/reference explained 43.91%, 34.25%, and 35.96% of the variation in ln biomass of C, N, and P respectively (Table 2.3). The median ( $\pm$  sd) mass of carbon was 1.28 ( $\pm$  0.74) moles and 0.17 ( $\pm$  0.88) moles in enclosures and references, respectively (Figure 2.4A). The largest difference in biomass of C between moose enclosure and reference occurred at Thorburn Lake, with a difference of 2.51 moles of C. The median ( $\pm$  sd) mass of N between moose enclosure and references was 0.014 ( $\pm$  0.012) moles and 0.002 ( $\pm$  0.010) moles respectively (Figure 2.4B). The largest difference in biomass of N also occurred at Thorburn Lake, with a difference of 0.041 moles of N. The median ( $\pm$  sd) mass of phosphorus was  $4.2 \times 10^{-4}$  ( $\pm 3.1 \times 10^{-4}$ ) moles and  $1.0 \times 10^{-4}$  ( $\pm 3.1 \times 10^{-4}$ ) moles in enclosures and references, respectively (Figure 2.4C). The trends in the biomass of K, Ca, Mg, Fe, Cu, Mn, Zn, and B are similar to the trends in C, N, and P and are presented in an appendix (Figure A.2). Disturbance regime and site predicted most of the variation in the biomass of C, N, and P (conditional  $R^2 = 0.64, 0.59, 0.59$  respectively).

The model with the fixed effect of moose enclosure/reference and random effects had a lower AIC than a model with only the random effects providing evidence that the C:N ratio of plant litter was influenced by the presence/absence of moose. The fixed effect of moose enclosure/reference explained 6.83% of the variation in C:N ratio (Table 2.3). The median ( $\pm$  sd) C:N ratio was 90.63 ( $\pm$  13.13) and 80.64 ( $\pm$  27.08) in enclosure and references, respectively (Figure 2.4E). Disturbance regime and site also explained a portion of variance in C:N ratio of plant litter (conditional  $R^2 = 0.08$ ). Like the top model for C:N ratio, the model with the fixed effect of enclosure/reference and random effects

had a lower AIC than the model with only random effects to explain variation in N:P ratio in litter biomass. However, the fixed effect of moose exclosure/reference explained very little of the variation of N:P ratio in plant litter (marginal  $R^2 = 0.0076$ ). The median ( $\pm$  sd) N:P ratio in plant litter was 31.32 ( $\pm$  3.8) and 31.90 ( $\pm$  7.8) in exclosure and references, respectively (Figure 2.4F). Disturbance regime and site explained more of the variation (conditional  $R^2 = 0.12$ ; Table 2.3).

*c. Soil nutrient quality*

For soil % C, both competing models (i.e.  $\Delta AIC < 2$ ) included the fixed effect of moose exclosure/reference, pH, and soil moisture, while the best model also included the term soil depth (Table 2.4). This provides some evidence that moose presence/absence and soil pH, moisture, and depth factors influenced variation in the % C in soils in our study area (Table A.11). The marginal  $R^2$  for the fixed effects in this top model were 0.001, 0.058, 0.386, and 0.031 for moose presence/absence, soil pH, soil moisture, and soil depth respectively. Soils in moose exclosures had a median ( $\pm$  sd) % C of 22.75 ( $\pm$  10.66) % while soils in reference areas had a median value of 20.6 ( $\pm$  13.78) % (Figure 2.5A). The greatest difference in percent C occurred at Fox Marsh 1 with an average difference of 2.95 %. The conditional  $R^2$  of our top model was 0.76, suggesting that the random effects of disturbance regime and site explained a larger portion of the variation in % C in soils.

For soil % N, the best model included the fixed effects of moose exclosure/reference and soil moisture, while a competing model also included the term soil depth (Table 2.4). This provides some evidence that moose presence/absence and soil moisture influenced variation in % N in soils in our study area (Table A.11). The marginal  $R^2$  for the fixed effects in the top model were 0.030, and 0.375 for moose

presence/absence and soil moisture. The median ( $\pm$  sd) % N in soils in exclosures and references was 0.785 ( $\pm$  0.26) % and 0.805 ( $\pm$  0.44) %, respectively (Figure 2.4B). The largest difference in percent N occurred at Port Blandford edge with an average difference of 0.63 %. The conditional  $R^2$  of our top model was 0.80, suggesting that the random effects of disturbance regime and site explained a large portion of the variation in % N in soils.

For soil % P, inclusion of any fixed effects led to a large reduction in model fit ( $\Delta AIC > 2$ ) indicating that the fixed effect of moose exclosure/reference and soil abiotic factors have little influence on variation in % P (Table 2.4). The median ( $\pm$  sd) % P of soils in moose exclosures and references was  $2.15e^{-3}$  ( $\pm$  sd) % and  $2.21e^{-3}$  ( $\pm$  sd), respectively (Figure 2.4C). The greatest difference in percent P occurred at Thorburn Lake with an average difference of  $2.62e^{-3}$  %.

The trends in the percent of K, Ca, Mg, Fe, Cu, Mn, Zn, and B in soils are similar to the trends in C, N, and P and are presented in an appendix (Figure A.3).

#### *d. Litter decomposition rates*

The average litter decomposition rate across all sites was 0.005 g/day (Figure 2.4D). However, decomposition rates varied across disturbance regimes with the slowest rates in sites that were disturbed by insects (0.001 g/day) and fastest rates in the balsam fir cut stands on the Avalon Peninsula and near Clarenville (0.004 g/day and 0.011 g/day) respectively.

For litter mass remaining, the top model included the fixed effect of time and had a lower AIC than models with the fixed effect of moose exclosure/reference and the interaction term (Table 2.5). Soil moisture was an explanatory variable in one of our top

models to explain litter decomposition rate but did not explain a significant portion of variation. Contrary to our hypothesis, litter mass remaining was not influenced by moose presence or absence (i.e. exclosure vs reference) (Table A.12). The marginal  $R^2$  for the fixed effect in the top model was 0.095. The conditional  $R^2$  of our top model was 0.44, suggesting that the random effects of disturbance regime and site explained a large portion of the variation in litter mass remaining.

## **2.5. Discussion**

Consumers play an important role in influencing key ecosystem processes, such as nutrient cycling and decomposition (Vanni 2002; Leroux & Loreau 2010; Schmitz et al. 2010). In other boreal systems, researchers have found that large ungulates impact the forest ecosystem through cascading effects from accelerated succession, thereby influencing important ecosystem processes (Risenhoover & Maas 1987; Brandner et al. 1990; McInnes et al. 1992; Pastor et al. 1993; Rossow et al. 1997; Pastor et al. 1998; Butler & Kielland 2007; DeJager & Pastor 2009). I set out to test the effects of an introduced ungulate, moose, on nutrient cycling and decomposition in previously disturbed forests of Newfoundland, Canada. Specifically, I compared plant composition, plant litter fall quantity and quality, soil quality and litter decomposition rates in 10 paired moose exclosures and references. I found evidence that moose absence allowed plants to grow taller and produce more litter biomass. Counter to findings in other systems, however, the diversity and composition of plants, litter quality (C:N ratio), soil quality and litter decomposition rates did not differ between moose exclosures and references.

I found evidence that exclusion of moose allowed for plant individuals to grow taller (Figure 2.3D). As moose continuously browse available plant material, they stunt sapling height and recruitment into the canopy. Researchers have shown that in areas of high moose density, preferred species, such as willow, white birch, trembling aspen and balsam fir, are significantly shorter than species found in areas of low moose density (Bergerund & Manuel 1968; Brandner et al. 1990; Thompson et al. 1992; Thompson & Curran 1993; Kielland & Bryant 1998). For example, Mathisen et al. (2010) found evidence that moose browsing in Sweden reduced the cover and reproductive growth of the preferred species, bilberry (*Vaccinium myrtillus*). I found evidence that the direct effect of moose browsing indirectly reduces the amount of plant litter biomass. In my study I found that preferred plants were 1.46X taller in exclosures than in references and the plant litter biomass was 7X greater in moose exclosures than in reference plots (Figure 2.2D & 2.4D). Research on white tailed deer and sika deer effects on litter biomass in Virginia, USA and on the Boso Peninsula, Japan, respectively, found a similar effect with greater litter biomass being produced in exclosures than in control plots (Bressette et al. 2012; Suzuki & Ito 2014). As a result of greater quantities of plant litter inside exclosures, the amount of available C, N, and P in litter biomass increased in the absence of moose (Figure 2.4 A, B, C). This is consistent with research findings on Isle Royale, where McInnes et al. (1992) found that litter C and N availability was directly correlated with plant biomass. Interestingly, however, I did not find that the quality of plant litter (C:N, N:P) differed between moose exclosure and reference plots.

The quality (C:N and N:P ratios) of litter material varies across plant species impacting the palatability (Bryant et al. 1991) and decomposability of plant material

(Flanagan and Van Cleve 1983; Pastor et al. 1993; Wardle et al. 2004). Contrary to our predictions and other studies (see review Wardle 2004), I did not find evidence for moose effects on plant species diversity or composition (Figure 2.3 A, B, C). The chemical make-up of individual species in our sites combined to influence litter quality, which did not differ between moose exclosure and control. The absence of a moose effect on plant diversity and composition has further implications for soil quality and litter decomposition rates. Specifically, the percent of carbon, nitrogen, and phosphorus in soils did not differ between moose presence and absence. Our results are counter to Pastor et al. (1993) who found that N mineralization rates were not dependent on the total amount of N entering soils, while litter quality did depress N mineralization, and Kielland and Bryant (1998) who found that soil C concentrations increased in areas of moose absence while total litter biomass remained the same between moose presence and absence. While the amount of C, N, and P entering the soils as litter in our study was greater in exclosures, it does not appear as though plant litter biomass per se impacts the percent of those elements in the soil. While our primary questions focused on woody trees and shrubs, I did measure the cover of other plant groups that may influence soil quality (e.g. grass and moss). Specifically, I found that % grass cover was 8X higher in controls than moose exclosures (Figure A.4) but had no discernable impact on soil quality differences between exclosure and control. Therefore it is likely that the biomass of C, N, and P in grass is not compensating for the quality (C:N and N:P) of plant material returning to soil, and as such, plant community composition may play a more important role in nutrient cycling in soils than the total amount of plant biomass. However, the % moss cover was similar across the exclosures and controls (Figure A.4) and may explain the similarities in



% C, % N, and % P in soils within a site as moss and lichens (not measured in our study) have higher availability of C and are able to fix more N (Blaško et al. 2015).

While I did not find evidence for moose effects on soil nutrient content, I did find evidence to suggest that abiotic components, such as soil pH, soil moisture, and soil depth are important factors influencing % C, % N, and % P in soils. Soil moisture, in particular, explained a sizeable amount of variation in the % C in soils (marginal  $R^2$  value of 0.39). Soil moisture was also an important predictor of % N in soil. Nitrogen availability is strongly correlated with soil temperature and moisture, factors that also influence microbial decomposition of soil matter (Frank 2008). Given similar soil nutrient contents in exclosures and controls, I suspect that soil fauna may also not differ among the treatments. As soil fauna is largely responsible for litter decomposition, it is not surprising then that I did not observe differences in litter decomposition rates between moose exclosures and controls. Available carbon in litter is typically recalcitrant, and therefore % C in soils may be more closely related to microbial decomposition rates than variation in C:N and N:P in litter biomass (Tanentzap & Coomes 2012). Variation in litter decomposition rates across our sites however, was partially explained by disturbance regime and site. I found decomposition rates varied across disturbance regimes, with faster rates of decomposition occurring in balsam fir cut stands on the Avalon Peninsula. Soil moisture was an explanatory variable in one of our top models to explain litter decomposition rate but did not explain a significant portion of variation. Persson et al. (2009) found that soil moisture did not affect soil respiration rates in boreal forests in Sweden. While moisture is likely a potential explanation for variation in the rate of decomposition of plant litter material, I may have not captured all of the variation in

moisture across our study sites. For example, Mayer (2008) demonstrated that decomposition rates varied across ecosystem types as a result of variation in moisture.

My findings are not entirely consistent with those other studies of moose effects on forest ecosystems, and I can offer three potential explanations for those differences. First, soil properties and disturbance regime explained a larger proportion of the variability in soil chemistry and decomposition rates. This may suggest that abiotic components may be a more important contributor to nutrient cycling in Newfoundland, Canada, then biotic factors, such as herbivore presence and plant species diversity. Newfoundland's climate is marine temperate, with a short growing season with seasonal temperatures and precipitation rates varying across the island. For example, in 2014 the average precipitation total on the Avalon Peninsula was approximately 1130 mm, while average number of days hitting at least 10°C were approximately 168 days a year (Government of Canada 2015). In TNNP in 2014, the temperature reached at least 10°C 143 days of the year and had 1100 mm of precipitation (Government of Canada 2015). In contrast, Isle Royale, located approximately 30 km off the north shore of Lake Superior, experience disturbance from fire in the 1930's, with an average of 750 mm of precipitation, and relatively deep soils (see Table A.13). Thus, local differences in climate along with variation in parent material, topography, disturbance regimes, and other abiotic factors seemingly influence key ecosystem processes of nutrient cycling and decomposition in Newfoundland and may explain differences between our study area and those in Isle Royale.

Second, our moose exclosures were established between 1995 and 1998 (Table 2.1), and my results report on 15-20 year old impacts of moose on forest ecosystems. At

the same time, studies on Isle Royale used exclosures that were ~40 years old (McInnes et al. 1992; Pastor et al. 1993; Pastor et al. 1998). Pastor et al. (1998) found that browsing by moose accelerates succession, shifting plant communities to spruce dominant forests, thereby reducing soil microbes and slowing decomposition which limits N availability to soils and uptake by plants. Research conducted in 18 year old exclosures found that exclusion of deer in oak-hickory forest in Virginia, USA, did cause a number of indirect effects including higher arthropod density and a decrease in soil nutrient content (Bressette et al. 2012). Unlike Virginia, Newfoundland experiences a short growing season which may slow down successional turnover. For example, Ellis (1960) indicated that plant growth of balsam fir and black spruce in Newfoundland is slow during the first ten to twenty years. A third potential explanation for limited indirect effects of moose is that we did not detect a moose effect while one may have been present. Future studies may consider using more moose exclosure/reference sites to increase the potential to detect small indirect effects of moose on forest ecosystems.

In conclusion, my research examined how herbivory induced changes in plant community composition might influence nutrient cycling. My models did not capture a significant portion of variation in nutrient dynamics in the province, suggesting that other mechanisms may be influencing nutrient returns. One possible explanation of residual variance in forest attributes with and without moose could be the effect of moose excreta or faeces on forest dynamics. Urine and faeces are considered one of the primary mechanisms in facilitating nitrogen mineralization in soils and feedbacks to plant communities (Bardgett and Wardle 2003). While urine and faeces accelerate nutrient return to communities, this return of nutrients is limited spatially and temporally. For

example, Cech et al. (2010) found that cattle redistribute reduced quantities of nutrients in urine and faeces than the nutrients cattle were consuming from plants. Steinauer and Collins (1995) found that where bovine urine was deposited nutrient returns increased within the patch itself but the effect was localized. However, Pastor et al. (1993) suggest that while the return of nutrients in moose urine and faeces is important, it does not compensate for long term changes in plant community composition in their Isle Royale study system.

My results indicate that moose presence affects the growth of trees and shrubs into the canopy and limits the production of litter biomass but that moose presence, at least in the time frame of my experiment, did not cause a cascading effect into soils in Newfoundland, Canada. This is counter to many long-term studies leaving us to wonder if moose effects are universal in other geographical regions. My study suggests abiotic factors such as disturbance history and soil moisture may have larger short term impacts on forest nutrient cycling in Newfoundland than the presence or absence of moose. Meta-analysis and further development of theory of ungulate effects on forest ecosystems may be a useful way to determine how or if the general findings of key long-term studies such as Isle Royale and Alaska apply to other regions.

## **2.6. References**

Bachand, M., S. Pellerin, M. Moretti, I. Aubin, J.P. Tremblay, S.D. Cote, M. Poulin.

2014. Functional responses and resilience of boreal forest ecosystem after reduction of deer density. PLoS ONE **9(2)**:e90437

- Bardgett, R.D., D.A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* **84**(9): 2258 - 2268
- Bardgett, R.D., D.A. Wardle, G.W. Yeates. 1998. Linking above-ground and below-ground interactions: How plant responses to foliar herbivory influence soil organisms. *Soil Biology & Biochemistry* **30**(14): 1867 - 1878
- Bates, D., M. Mäechler, B.M. Bolker, S. Walker. 2015. Lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-9, <https://cran.r-project.org/Ib/packages/lme4/index.html>
- Bell, T. 2002. Ecoregions of Newfoundland. Heritage Newfoundland & Labrador. <<http://www.heritage.nf.ca/articles/environment/ecoregions-newfoundland.php>>
- Bergerud, A.T., F. Manuel. 1968. Moose damage to balsam fir-white birch forests in central Newfoundland. *The Journal of Wildlife Management* **32**(4): 729 - 746
- Blaško, R., L.H. Bach, S.A. Yarwood, S.E. Trumbore, P. Högberg, M.N. Högberg. 2015. Shifts in soil microbial community structure, nitrogen cycling and the concomitant declining N availability in ageing primary boreal forest ecosystems. *Soil Biology and Biochemistry* **91**: 200 – 211
- Boland, T. 2011. Trees and Shrubs of Newfoundland and Labrador: field guide. Boulder Publications: Portugal Cove-St. Philip's, Canada
- Brandner, T.A., R.O. Peterson, K.L. Risenhoover. 1990. Balsam fir on Isle Royale: Effects of moose herbivory and population density. *Ecology* **71**: 155 – 164
- Bressette, J.W., H. Beck, V.B. Beauchamp. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. *Oikos* **121**: 1749 – 1760

- Bump, J.K., C.R. Webster, J.A. Vucetich, R.O. Peterson, J.M. Shields, M.D. Powers. 2009. Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage. *Ecosystems* **12**: 996 – 1007
- Butler, L.G., K. Kielland. 2008. Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. *Journal of Ecology* **96**: 136 - 144
- Carline, K.A., H.E. Jones, R.D. Bardgett. 2005. Large herbivores affect the stoichiometry of nutrients in a regenerating woodland ecosystem. *Oikos* **110**: 453 - 460
- Connor, K.J., W.B. Ballard, T. Dilworth, S. Mahoney, D. Anions. 2000. Changes in structure of a boreal forest community following intense herbivory by moose. *Alces* **36**: 111 – 132
- Côté, S.D., J. Beguin, S. de Bellefeuille, E. Champagne, N. Thiffault, J.P. Tremblay. 2014. Structuring effects of deer in boreal forest ecosystems. *Advances in Ecology*. Article ID 917834
- Dodds, D.G. 1960. Food competition and range relationships of moose and snowshoe hare in Newfoundland. *Journal of Wildlife Management* **24(1)**: 52 – 60
- De Jager, N.R., J. Pastor. 2009. Declines in moose population density at Isle Royale National Park, MI, USA and accompanied changes in landscape patterns. *Landscape Ecology* **24**: 1389 – 1403
- Edenius, L., M. Bergman, G. Ericsson, K. Danell. 2002. The role of moose as a disturbance factor in managed boreal forests. *Silva Fennica* **36(1)**: 57 - 67
- Ellis, R.C. 1960. Final report: An investigation of the length of regeneration period and of the yield potential of pulpwood cut-overs in Newfoundland. Department of

- Northern Affairs and National Resources Forestry Branch. Project NF 47. St. John's, Newfoundland
- Elser, J.J., R.W. Sterner, E. Gorokhova, W.F. Fagan, T.A. Markow, J.B. Cotner, J.F. Harrison, S.E. Hobbie, G.M. Odell, L.J. Weider. 2000. Biological stoichiometry from genes to ecosystems. *Ecology Letters* **3**: 540 – 550
- Flanagan, P.W., K. van Cleve. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. *Canadian Journal of Forest Research* **13**: 795 - 817
- Fornara, D.A., J.T. Du Toit. 2008. Browsing-induced effects on leaf litter quality and decomposition in a southern African savanna. **11**: 238 – 249
- Frank, D.A. 2008. Ungulate and topographic control of nitrogen: phosphorus stoichiometry in a temperate grassland; soils, plants and mineralization rates. *Oikos* **117**: 591 - 601
- Gosse, J., L. Hermanutz, B. McLaren, P. Deering, T. Knight. 2011. Degradation of boreal forests by non-native herbivores in Newfoundland's National Parks: Recommendations for ecosystem restoration. *Natural Areas Journal* **31**: 331 – 339
- Government of Canada. 2015. Newfoundland and Labrador – Weather Conditions and Forecast by Locations. <  
[https://weather.gc.ca/forecast/canada/index\\_e.html?id=NL](https://weather.gc.ca/forecast/canada/index_e.html?id=NL)>
- Haynes, A.G., M. Schutz, N. Buchmann, D.S. Page-Dumroese, M.D. Busse, A.C. Risch. 2014. Linkages between grazing history and herbivore exclusion on decomposition rates in mineral soils of subalpine grasslands. *Plant Soil* **374**: 579 - 591

- Hester, A.J., M. Bergman, G.R. Iason, J. Moen. 2006. Impacts of large herbivores on plant community structure and dynamics. In K. Danell, R. Bergstrom, P. Duncan, and J. Pastor (Eds.) *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (97-141). Cambridge, UK: Cambridge University Press
- Hobbs, N.T. 1996. Modification of ecosystems by ungulates. *The Journal of Wildlife Management* **60**: 695 – 713
- Humber, J.M., L. Hermanutz. 2011. Impacts of non-native plant and animal invaders on gap regeneration in a protected boreal forest. *Biological Invasions* **13**: 2361 – 2377
- Johnson, D., L. Kershaw, A. MacKinnon, J. Pojar. 2009. *Plants of the Western Forest: Alberta, Saskatchewan, & Manitoba Boreal and Aspen Parkland*. Lone Pine Publishing: Edmonton, Alberta
- Joyce, T.L., S.P. Mahoney. 2001. Spatial distributions of moose-vehicle collisions in Newfoundland. *Wildlife Society Bulletin* **29(1)**: 281 – 291
- Kielland, K., J.P. Bryant. 1998. Moose herbivory in Taiga: Effects of biogeochemistry and vegetation dynamics in primary succession. *Oikos* **82(2)**: 377 - 383
- Leriche, H., X. LeRoux, J. Gignoux, A. Tuzet, H. Fritz, L. Abbadie, M. Loreau. 2001. Which functional processes control the short-term effect of grazing on net primary production in grasslands? *Oecologia* **129**: 114 – 124
- Leroux, S.J., M. Loreau. 2010. Consumer-mediated recycling and cascading trophic interactions. *Ecology* **91(7)**: 2162 – 2171
- Leroux, S.J., O.J. Schmitz. 2015. Predator-driven element cycling: the impact of predation and risk effects on ecosystem stoichiometry. *Ecology and Evolution* **5(21)**: 4976 – 4988



- Mathisen, K.M., F. Buhtz, K. Danell, R. Bergstrom, C. Skarpe, O. Suominen, I.L. Persson. 2010. Moose density and habitat productivity affects reproduction, growth and species composition in field layer vegetation. *Journal of Vegetation Science* **21**: 705 - 716
- Mayer, P.M. 2008. Ecosystem and decomposer effects on litter dynamics along an old field to old-growth forest successional gradient. *Acta Oecologica* **33**: 222 – 230
- McInnes, P.F., R.J. Naiman, J. Pastor, Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* **73**: 2059 – 2075
- McLaren, B., L. Hermanutz, J. Gosse, B. Collet, C. Kasimos. 2009. Broadleaf competition interferes with balsam fir regeneration following experimental removal of moose. *Forest Ecology and Management* **257**: 1395 – 1404
- Molvar, E.M., R.T. Bowyer, V. Van Ballenberghe. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. *Oecologia* **94**: 472 – 479
- Murray, B.D., C.R. Webster, J.K. Bump. 2013. Broadening the ecological context of ungulate-ecosystem interactions: the importance of space, seasonality, and nitrogen. *Ecology* **94**: 1317 – 1326
- Naiman, R.J., C.A. Johnston, J.C. Kelley. 1988. Alteration of North American streams by beaver. *BioScience* **38**: 753 – 762
- Newfoundland and Labrador Wildlife Division. 2015. 2015 – 2020 Newfoundland and Labrador Moose Management Plan. Department of Environment and Conservation <[http://www.env.gov.nl.ca/env/moose\\_plan.pdf](http://www.env.gov.nl.ca/env/moose_plan.pdf)>

- Nuttle, T., E.H. Yerger, S.H. Stoleson, T.E. Ristau. 2011. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. *Ecosphere* **2**: article 4
- Oksanen, J., G.F. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, H. Wagner. 2015. Package 'vegan'. R package version 2.3-1, <https://github.com/vegandevs/vegan>
- Olofsson, J., L. Oksanen. 2002. Role of litter decomposition for the increased primary productivity in areas heavily grazed by reindeer: A litterbag experiment. *Oikos* **96**: 507 – 515
- Pace, M.L., J.J. Cole, S.R. Carpenter, J.F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *TREE* **14(12)**: 483 – 488
- Pastor, J., B. Dewey, R. Moen, D.J. Mladenoff, M. White, Y. Cohen. 1998 Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA. *Ecological Applications* **8**: 411 – 424
- Pastor, J., B. Dewey, R.J. Naiman, P.F. McInnes, Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* **74**: 467 – 480
- Pastor, J., R.J. Naiman, B. Dewey, P. McInnes. 1988. Moose, microbes, and the boreal forest. *BioScience* **38**: 770 – 777
- Persson, I.L., M.B. Nilsson, J. Pastor, T. Eriksson, R. Bergstrom. 2009. Depression of belowground respiration rates at simulated high moose population densities in boreal forests. *Ecology* **90(10)**: 2724 - 2733

- Pimlott, D. 1953. Newfoundland Moose. North American Wildlife Conference: Transactions **18**: 563 – 581
- Polis, G.A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* **86**: 3 – 15
- Rae, L.F., D.M. Whitaker, I.G. Warkentin. 2013. Multiscale impacts of forest degradation through browsing by hyperabundant moose (*Alces alces*) on songbird assemblages. Diversity and Distributions DOI: 10.1111/ddi.12133
- Risenhoover, K.L., S.A. Maass. 1987. The influence of moose on the composition and structure of Isle Royale forests. *Canadian Journal of Forest Research* **17**: 357 – 364
- Rooney, T., D.M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* **181**: 165 – 176
- Rossow, L.J., J.P. Bryant, K. Kielland. 1997. Effects of above-ground browsing by mammals on mycorrhizal infection in an early successional taiga ecosystem. *Oecologia* **110**: 94 – 98
- Rotter, M.C., A.J. Rebertus. 2015. Plant community development of Isle Royale's moose-spruce savannas. *Botany* **93(2)**: 75 – 90
- Sankaran, M., D.J. Augustine. 2004. Large herbivores suppress decomposer abundance in a semiarid grazing ecosystem. *Ecology* **85(4)**: 1052 – 1061
- Schmitz, O.J., D. Hawlena, G.C. Trussell. 2010. Predator control of ecosystem nutrient dynamics. *Ecology Letters* **13(10)**: 1199 – 1209
- Sørensen, L.I., J. Mikola, M.M. Kytöviita, J. Olofsson. 2009. Trampling and spatial heterogeneity explain decomposer abundances in a sub-arctic grassland subjected to simulated reindeer grazing. *Ecosystems* **12**: 830 – 842

- Stark, S., D.A. Wardle, R. Ohtonen, T. Helle, G.W. Yeates. 2000. The effect of reindeer grazing on decomposition, mineralization and soil biota in a dry oligotrophic Scots pine forest. *Oikos* **90**(2):301 - 310
- Steinauer, E.M., S.L. Collins. 1995. Effects of urine deposition on small-scale patch structure in prairie vegetation. *Ecology* **76**: 1195 – 1205
- Suzuki, M., E. Ito. 2014. Combined effects of gap creation and deer exclusion on restoration of belowground systems of secondary woodlands: A field experiment in warm-temperate monsoon Asia. *Forest Ecology and Management* **329**: 227 - 236
- Synder, J.D., R.A. Janke. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. *The American Midland Naturalist* **95**(1): 79 – 92
- Tabuchi, K., D.T. Quiring, L.E. Flaherty, L.L. Pinault, K. Ozaki. 2011. Bottom-up trophic cascades caused by moose browsing on a natural enemy of galling insect on balsam fir. *Basic and Applied Ecology* **12**: 523 - 531
- Tanner, A.L., S.J. Leroux. 2015. Effect of roadside vegetation cutting on moose browsing. *PLoS One* DOI: 10.1371/journal.pone.0133155
- Tanzentzap, A.J., D.A. Coomes. 2012. Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? *Biological Reviews* **87**: 72 - 94
- Teichman, K.J., S.E. Nielsen, J. Roland. 2013. Trophic cascades: linking ungulates to shrub-dependent birds and butterflies. *Journal of Animal Ecology* **82**: 1288 - 1299
- Thompson, I.D., A.U. Mallik. 1989. Moose browsing and allelopathic of *Kalmia angustifolia* on balsam fir regeneration in central Newfoundland. *Canadian Journal of Forest Research* **19**: 524 - 526

- Thompson, I.D., W.J. Curran. 1993. A re-examination of moose damage to balsam fir – white birch forests in central Newfoundland: 27 years later. *Canadian Journal of Forest Research* **23**: 1388 – 1395
- Thompson, I.D., W.J. Curran, J.A. Hancock, C.E. Butler. 1992. Influence of moose browsing on successional forest growth on black spruce sites in Newfoundland. *Forest Ecology and Management*. **47**: 29 – 37
- Van Cleve, K., F.S Chapin III, C.T. Dyrness, L.A. Viereck. 1991. Element cycling in taiga forests: State-factor control. *BioScience* **41**: 78 – 88
- Vanni, M.J. 2002. Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* **33**: 341 – 370
- Wardle, D.A., G.M. Barker, G.W. Yeates, K.I. Bonner, A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forests: Aboveground and belowground consequences. *Ecological Monographs* **71(4)**: 587 - 614
- Wardle, D.A., K.I. Bonner, G.M. Barker. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology* **16(5)**: 585 - 595
- Wardle, D.A., R.B. Bardgett, J.N. Klironomos, H. Setälä, W.H. van der Putten, D.H. Wall. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**: 1629 - 1633
- Yates, C.J., D.A. Norton, R.J. Hobbs. 2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-Western Australia: implications for restoration. *Austral Ecology* **25**: 36 – 47

**Table 2. 1:** Coordinates of paired exclosure and reference plots used in Newfoundland, Canada. Sites were sampled in 2014 and are grouped according to disturbance regime/dominant habitat.

Location	Date Established	Site Name	Latitude	Longitude	Site descriptors
Avalon Peninsula	1995	Fox Marsh 1	N 47.37193	W -53.42772	Balsam fir dominant, clear cut in early 1990's
		Fox Marsh 2	N 47.35927	W -53.39473	
Clareville	1998	Port Blandford centre	N 48.37596	W -54.08458	Balsam fir dominant, clear cut in early 1990's
		Port Blandford edge	N 48.37693	W -54.08522	
		Thorburn Lake	N 48.30362	W -54.14200	
TNNP*	1998	Blue Hill centre	N 48.60003	W -53.96815	Disturbed by insects in 1970's, open spruce moose savannah
		Blue Hill edge	N 48.59968	W -53.96888	
		Blue Hill West	N 48.58922	W -53.99335	Disturbed by insects in 1970's, spruce dominant forest
		Ochre Hill	N 48.50963	W -53.95678	Disturbed by insects in 1970's and again by Hurricane Igor in 2010, open canopy
		Platters Cove	N 48.42692	W -54.10883	

\*TNNP = Terra Nova National Park

**Table 2. 2:** Two general linear mixed effects models to determine if plant composition differs between moose exclosure/control in Newfoundland, Canada. I fit each model using seven different response variables to test moose exclosure/control effects: species diversity (measured as Shannon Wiener index); number of preferred and non-preferred species; number of preferred and non-preferred individual plants; and height of preferred and non-preferred individuals. I included site nested in disturbance regime as random variables in each model.

Response	Model rank	Description	k	LL	$\Delta AIC_c$	$\omega AIC_c$	Marginal $R^2$	Conditional $R^2$
Species diversity	1	1 + (1 Disturbance regime/Site)	4	-14.48	0.00	0.93	na	0.64
	2	Exclosure/Control + (1 Disturbance regime/Site)	5	-15.28	5.22	0.069	0.0045	0.62
Number of preferred species	1	1 + (1 Disturbance regime/Site)	4	-37.94	0.00	0.81	na	0.59
	2	Exclosure/Control + (1 Disturbance regime/Site)	5	-37.57	2.87	0.19	0.00	0.56
Number of non-preferred species	1	1 + (1 Disturbance regime/Site)	4	-23.063	0.00	0.88	na	0.21
	2	Exclosure/Control + (1 Disturbance regime/Site)	5	-23.07	3.94	0.12	0.004	0.16
Number of preferred individuals	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-88.34	0.00	0.82	0.0009	0.23
	2	1 + (1 Disturbance regime/Site)	4	-91.68	3.065	0.178	na	0.28
Number of non-preferred individuals	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-85.63	0.00	0.97	0.13	0.30
	2	1 + (1 Disturbance regime/Site)	4	-91.06	6.92	0.030	na	0.14
Height of	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-2748.21	0.00	1	0.13	0.32

preferred individuals	2	regime/Site)						
		1 + (1 Disturbance regime/Site)	4	-2790.46	82.46	0	na	0.21
Height of non-preferred individuals	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-4167.21	0.00	1	0.086	0.18
	2	1 + (1 Disturbance regime/Site)	4	-4193.53	50.62	0	na	0.25

k, number of parameters; LL, log-likelihood; AIC<sub>c</sub>, Akaike information criterion,  $\Delta$ AIC<sub>c</sub>, difference in AIC between most

parsimonious model and subsequent models;  $\omega$ AIC<sub>c</sub>, weight of models



**Table 2. 3:** Mixed effects models to determine if plant litter quantity and nutrient quantity was different between moose exclosures/control in Newfoundland, Canada. I used 6 response variables to test moose exclosure/control effects: plant litter biomass; molar mass of C, N, and P in plant litter; and C:N ratio and N:P ratio in plant litter biomass. I included site nested in disturbance regime as a random variable in our models.

Response	Model rank	Description	k	LL	$\Delta AIC_c$	$\omega AIC_c$	Marginal $R^2$	Conditional $R^2$
Plant litter biomass	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-27.75	0.00	0.99	0.45	0.66
	2	1 + (1 Disturbance regime/Site)	4	-34.58	10.05	0.01	na	$1.66e^{-15}$
Carbon	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-28.44	0.00	0.99	0.44	0.64
	2	1 + (1 Disturbance regime/Site)	4	-34.99	9.49	0.0086	na	0.00
Nitrogen	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-29.93	0.00	0.96	0.34	0.59
	2	1 + (1 Disturbance regime/Site)	4	-35.09	6.69	0.034	na	0.033
Phosphorus	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-29.33	0.00	0.97	0.36	0.59
	2	1 + (1 Disturbance regime/Site)	4	-34.77	7.26	0.026	na	0.063
C:N ratio	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-82.88	0.00	0.89	0.068	0.083
	2	1 + (1 Disturbance regime/Site)	4	-86.75	4.12	0.11	na	0.00
N:P ratio	1	Exclosure/Control + (1 Disturbance regime/Site)	5	-60.45	0.00	0.53	0.0076	0.12
	2	1 + (1 Disturbance regime/Site)	4	-62.39	0.26	0.47	na	0.15

k, number of parameters; LL, log-likelihood;  $AIC_c$ , Akaike information criterion,  $\Delta AIC_c$ , difference in AIC between most parsimonious model and subsequent models;  $\omega AIC_c$ , weight of models

**Table 2. 4:** Results of model selection to determine if the % of C, N, and P differed between moose exclosures/control in Newfoundland, Canada. I included site nested in disturbance regime as a random variable in all models.

	Model rank	Description	k	LL	$\Delta AIC_c$	$\omega AIC_c$	Marginal $R^2$	Conditional $R^2$
Carbon	1	Exclosure/Control + Soil pH + Soil moisture + Soil depth + (1 Disturbance regime/Site)	8	-262.53	0.00	0.63	0.39	0.76
	2	Exclosure/Control + Soil pH + Soil moisture + (1 Disturbance regime/Site)	7	-264.33	1.12	0.36	0.40	0.76
	3	Exclosure/Control + Soil moisture + Soil depth + (1 Disturbance regime/Site)	7	-269.55	11.53	0.0020	0.37	0.75
	4	Exclosure/Control + Soil moisture + (1 Disturbance regime/Site)	6	-270.75	11.54	1.00	0.39	0.74
	5	Exclosure/Control + Soil pH + (1 Disturbance regime/Site)	6	-291.61	11.54	1.00	0.059	0.46
	6	Exclosure/Control + Soil depth + Soil pH + (1 Disturbance regime/Site)	7	-291.06	54.58	1.00	0.087	0.48
	7	Exclosure/Control + (1 Disturbance regime/Site)	5	-300.28	68.24	1.00	0.0010	0.40
	8	Exclosure/Control + Soil depth + (1 Disturbance regime/Site)	6	-299.25	68.52	1.00	0.032	0.40
	9	1 + (1 Disturbance regime/Site)	4	-302.04	69.50	1.00	na	0.40
Nitrogen	1	Exclosure/Control + Soil moisture + (1 Disturbance regime/Site)	6	1.96	0.00	0.57	0.40	0.80
	2	Exclosure/Control + Soil moisture + Soil depth + (1 Disturbance regime/Site)	7	2.71	0.89	0.94	0.46	0.77

	3	Exclosure/Control + pH + Soil moisture + (1 Disturbance regime/Site)	7	0.55	5.25	0.55	0.42	0.78
	4	Exclosure/Control + Soil pH + Soil moisture + Soil depth + (1 Disturbance regime/Site)	8	0.80	7.22	1.00	0.47	0.76
	5	1 + (1 Disturbance regime/Site)	4	-25.68	50.65	1.00	na	0.36
	6	Exclosure/Control + (1 Disturbance regime/Site)	5	-25.56	52.69	1.00	0.030	0.39
	7	Exclosure/Control + Soil pH + 1 Disturbance regime/Site)	6	-26.63	57.19	1.00	0.035	0.40
	8	Exclosure/Control + Soil depth + (1 Disturbance regime/Site)	6	-29.05	62.00	1.00	0.031	0.40
	9	Exclosure/Control + Soil depth + Soil pH + (1 Disturbance regime/Site)	7	-30.05	66.43	1.00	0.036	0.41
	1	1 + (1 Disturbance regime/Site)	4	412.42	0.00	0.99	na	0.59
	2	Exclosure/Control + (1 Disturbance regime/Site)	6	400.36	16.70	0.0002	0.0016	0.67
Phosphorus	3	Exclosure/Control + Soil moisture + (1 Disturbance regime/Site)	6	400.69	28.67	0.00	0.011	0.69
	4	Exclosure/Control + Soil depth + (1 Disturbance regime/Site)	6	397.94 3	34.17	0.00	0.031	0.40
	5	Exclosure/Control + Soil pH + (1 Disturbance regime/Site)	6	394.71	40.64	0.00	0.0081	0.66
	6	Exclosure/Control + Soil moisture + Soil depth + (1 Disturbance regime/Site)	7	394.37	43.72	0.00	0.051	0.67
	7	Exclosure/Control + Soil pH + Soil moisture + (1 Disturbance regime/Site)	7	389.85	52.79	0.00	0.015	0.68
	8	Exclosure/Control + Soil depth + Soil	7	386.77	58.95	0.00	0.036	0.41

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	pH + (1 Disturbance regime/Site)						
9	Exclosure/Control + Soil pH + Soil moisture + Soil depth + (1 Disturbance regime/Site)	8	382.91	69.13	0.00	0.056	0.67

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k, number of parameters; LL, log-likelihood; AIC<sub>c</sub>, Akaike information criterion,  $\Delta$ AIC<sub>c</sub>, difference in AIC between most parsimonious model and subsequent models;  $\omega$ AIC<sub>c</sub>, Weight of model

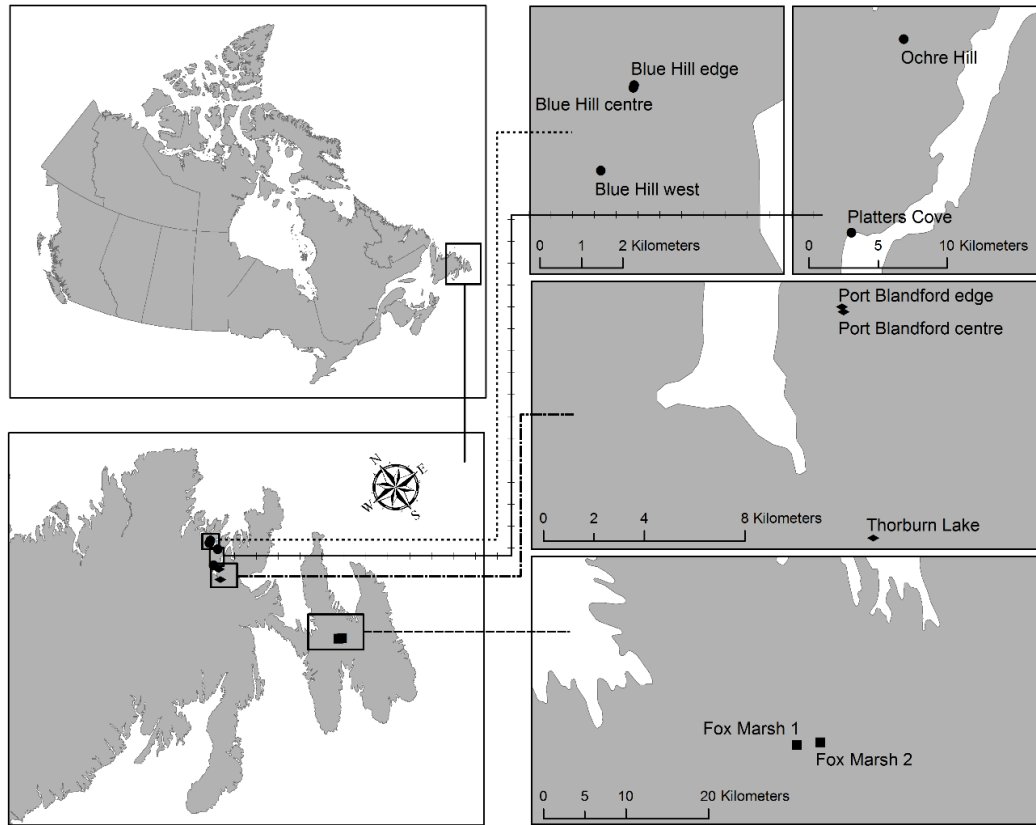
**Table 2. 5:** The results of the top three (out of 13) general linear mixed effects models to determine how mass remaining was affected by site, exclosure/control, disturbance regime and site in Newfoundland, Canada. Models included have a  $\Delta AIC_c < 8$ .

Data was collected from August 1 to November 9, 2014. The null model is included with its ranking.

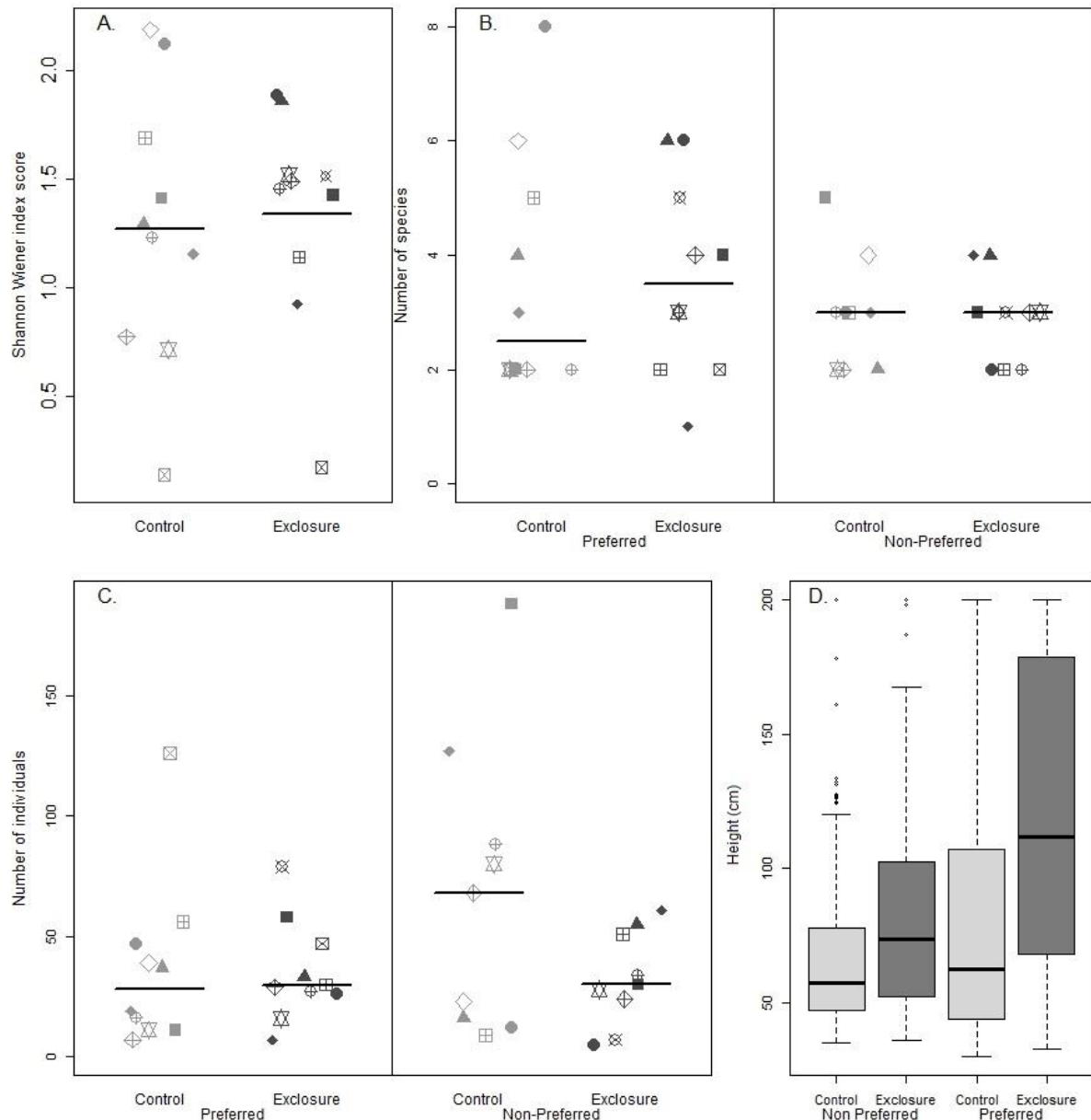
Model	Description	k	LL	$\Delta AIC_c$	$\omega AIC_c$	Marginal $R^2$	Conditional $R^2$
1	Time + (1 Disturbance regime/Site)	5	-36.93	0.0000	0.7791	0.0952	0.4412
2	Time + Soil Moisture + (1 Disturbance regime/Site)	6	-37.51	3.2781	0.1513	0.0948	0.4408
3	Time + Exclosure/Control + (1 Disturbance regime/Site)	6	-38.72	5.6910	0.0453	0.0979	0.4445
10	1 + (1 Disturbance regime/Site)	4	-48.43	20.91	0.0000	na	0.3615

k, number of parameters; LL, log-likelihood;  $AIC_c$ , Akaike information criterion,  $\Delta AIC_c$ , difference in AIC between most

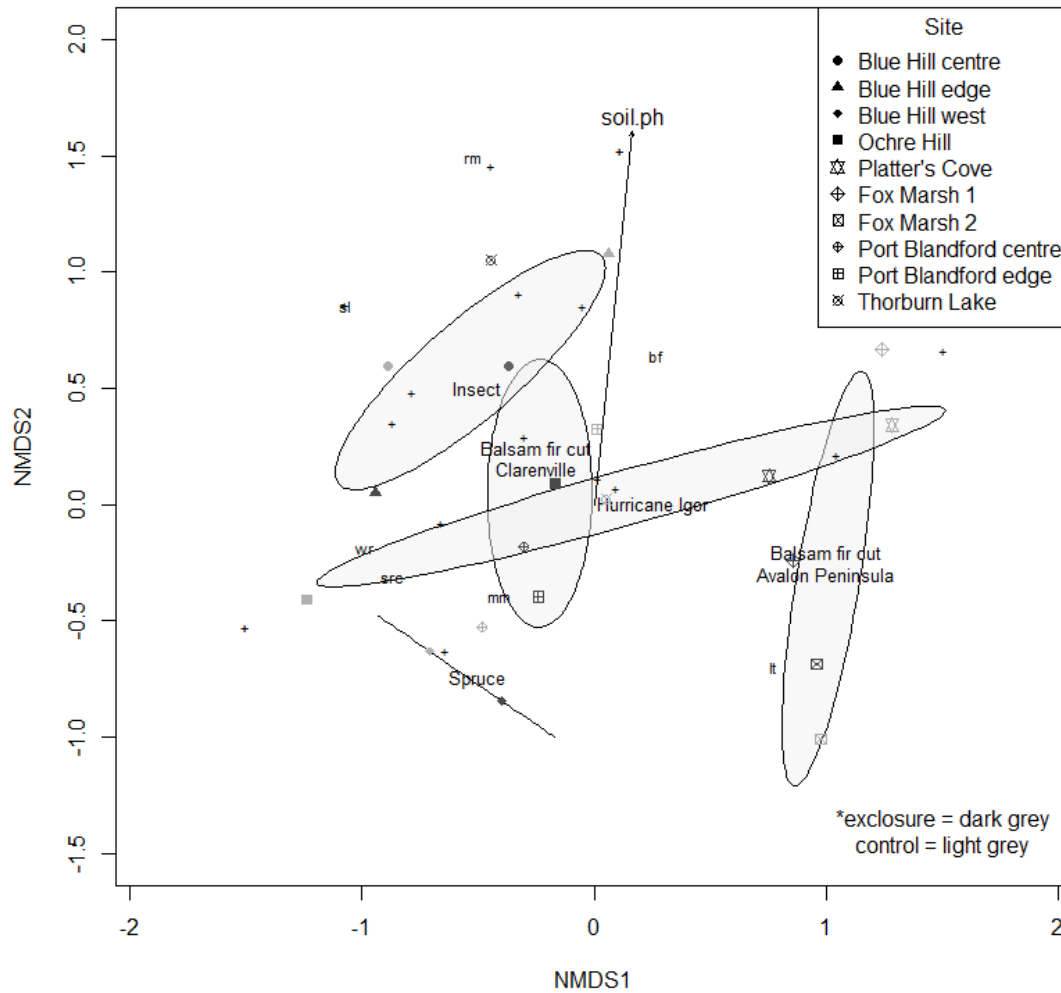
parsimonious model and subsequent models;  $\omega AIC_c$ , weight of models



**Figure 2. 1:** The locations of 10 paired exclosure-control sites in Newfoundland, Canada. Five sites were located in Terra Nova National Park (TNNP), three were near Clarenville, and two occurred on the Avalon Peninsula. Sites were found within 5 different disturbance regimes. Blue Hill centre and edge were disturbed by insects in the 1970's. Blue Hill west was found in a spruce dominant forest disturbed by insects in the 1970's. Ochre Hill and Platters Cove are found in a mixed canopy disturbed by insects in 1907's and Hurricane Igor in 2010. Port Blandford centre, edge and Thorburn Lake occur in a balsam fir stand that was logged in the 1990's, while Fox Marsh 1 and 2 occur in a balsam fir stand logged in 1995.

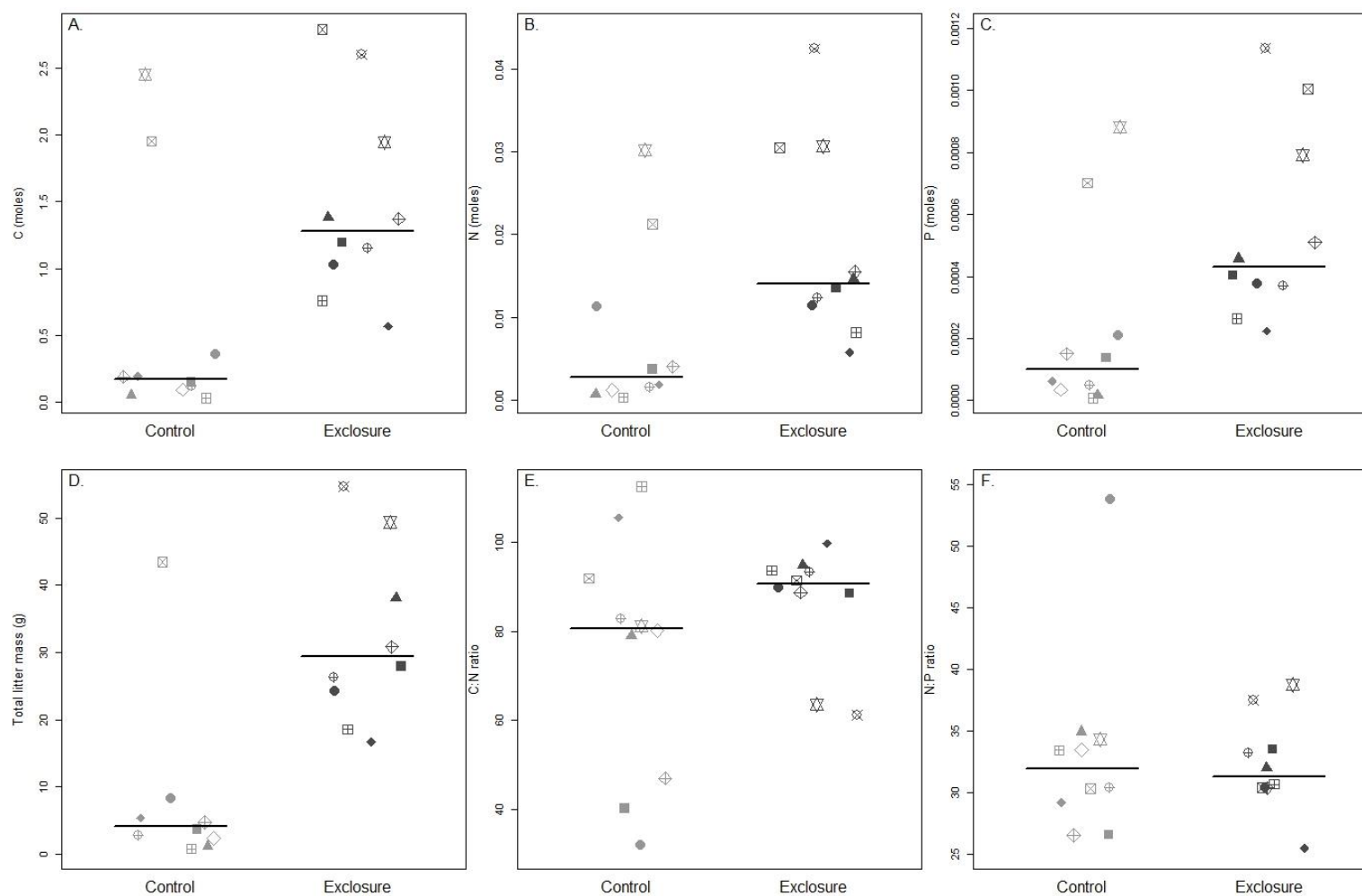


**Figure 2. 2:** A) The diversity of moose exclosures and controls in Newfoundland, Canada. B) The number of preferred and non-preferred species found in moose exclosures and controls. C) The number of preferred and non-preferred individuals found in moose exclosures and controls. D) The height of preferred and non-preferred individuals found in moose exclosures and controls.

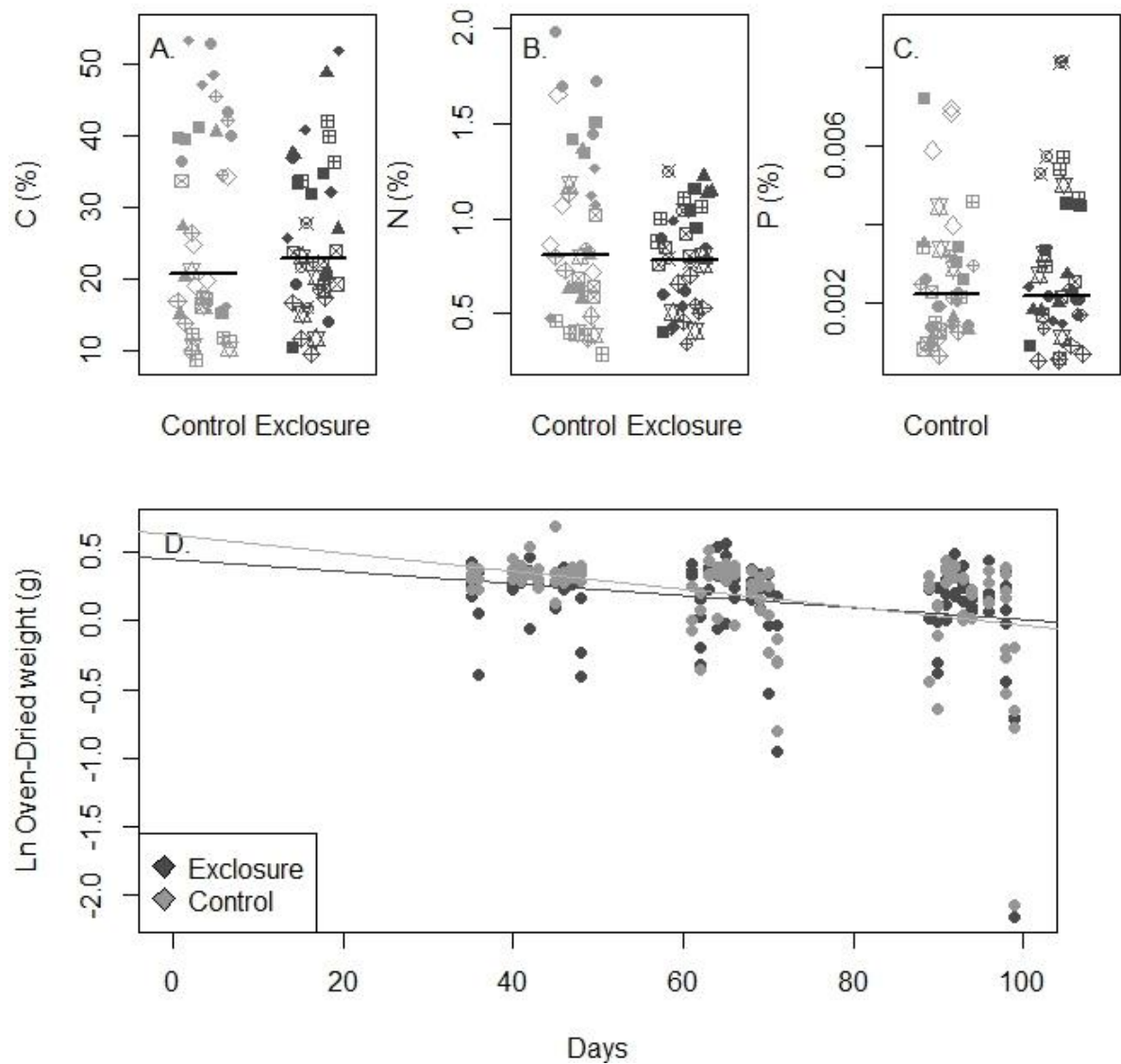


**Figure 2. 3:** Nonmetric multidimensional scaling plot (with Bray-Curtis distance) illustrating variation in plant species composition and abundance among 10 study sites and 5 disturbance regimes in Newfoundland, Canada. Each site is represented by a different symbol, and paired enclosure/control are displayed in different colours. Only plant species with a  $|r| > 0.423$  (Upton and Cook 2008) are displayed as the following: bf = balsam fir; lt = Labrador tea; mm = mountain maple; rm = red maple; sb = service berry; sl = sheep laurel; src = swamp red currant; wr = wild raspberry. All remaining plant species are indicated by a “+”. Environmental variables are indicated using an arrow, with length and direction indicating the correlation with the axes.





**Figure 2. 4:** The molar mass (in moles) of A) carbon, B) nitrogen, and C) phosphorus found in plant litter fall in moose exclosures and controls in Newfoundland, Canada. D) The biomass of plant litter fall found in moose exclosures and controls. The E) C: N ratio and F) N: P ratio found in moose exclosure and controls.



**Figure 2. 5:** The % of A) carbon, B) nitrogen, and C) phosphorus found in soils compared between moose exclosures and controls in Newfoundland, Canada. D) The oven dry Weight remaining (g) of decomposition bags placed in moose exclosures or control plots. Samples were collected over three time periods, the first after 35 – 47 days, the second after 61 – 70 days, and the final collection period 89 – 98 days.

## **CHAPTER 3: Summary and Conclusions**

### **3.1. Moose effects on nutrient cycling**

Consumers make decisions on resource acquisition as they require specific ratios of elements to maintain fitness and reproductive efforts (McIntyre & Flecker 2010). These complex foraging decisions can alter ecosystem structure and function. As a result, consumers can have large direct and indirect effects influencing savannahs (Asner & Levick 2012), alpine grasslands (Haynes et al. 2014), temperate forests (Niwa et al. 2011), streams (Naiman et al. 1988), and other terrestrial, freshwater, and marine environments.

Herbivore feeding preferences can influence key aboveground and belowground ecosystem processes (Wardle et al. 2004). For example, grazers can decelerate succession stimulating compensatory growth of forage grasses and herbs (Verchot et al. 2002). Browsers on the other hand, can accelerate succession, promoting the growth of non-preferred plant species (Bressette et al. 2012). For example, researchers have found that moose alter plant community composition from nutrient rich plants to nutrient poor ones. Moose have been found to shift willow dominant stands to alder in Alaska (Kielland & Bryant 1998) and balsam fir forests to black spruce in Isle Royale (McInnes et al. 1992). As nutrient poor plant biomass is returned to the soil, decomposition is retarded, which limits the available carbon, nitrogen, phosphorus, and other trace elements to the soil ecosystem. In turn, nutrient cycling in areas under moose browsing is reduced and in some instances has caused negative effects on species of birds, insects, and invertebrate communities. For example, Teichman et al. (2013) found that moose and other ungulates

reduced available shrub cover, negatively effecting shrub-dependent birds and butterflies. I studied the effects of introduced moose on previously disturbed boreal forest of Newfoundland, Canada to examine if global trends of ungulates hold true in a province with no natural predators. Specifically, I conducted an experiment to determine if moose influenced plant community composition, litter fall quantity and quality, soil quality, and litter decomposition rates. I used approximately 20 year old paired exclosure-control plots; the following results were consistent with my predictions:

- Preferred and non-preferred plant individual growing in moose exclosures were taller than preferred and non-preferred individuals growing in references
- Plant litter biomass in moose exclosures was greater than plant litter biomass in references
- The mass of carbon, nitrogen, and phosphorus was greater in moose exclosures than in references

These results are consistent with other research on ungulate effects. Thompson et al. (1992) found balsam fir, trembling aspen, and white birch were taller within moose exclosures than outside. Similar trends have been seen on Isle Royale, where moose suppress growth of balsam fir (Brandner et al. 1990) thereby leading to reduced plant litter biomass and limiting the amount of available carbon and nitrogen entering the soil (McInnes et al. 1992). Other ungulate species, such as white tailed deer (Bressette et al. 2012), red deer (Mason et al. 2010), and sika deer (Suzuki & Ito 2014), show similar effects on plant height and biomass production.

While I found moose effects on plant height, plant litter biomass, and mass of nutrients which were consistent with my predictions, I did not find support for my hypotheses related to plant diversity, soil quality, and litter decomposition rates.

Specifically:

- Plant species diversity and the number of preferred and non-preferred species and individuals did not differ between moose exclosures and controls
- The carbon: nitrogen ratio and nitrogen: phosphorus ratio did not differ between moose exclosures and controls
- The percent carbon, nitrogen, and phosphorus in soils did not differ between moose exclosures and controls
- Litter decomposition rates did not differ between moose exclosures and controls.

These findings are contrary to other studies. For example, Mathisen et al. (2010) found that plant diversity decreased by 10% in comparison areas having either zero to five moose per km<sup>2</sup> in Sweden. Research in Newfoundland has shown that the density of coniferous trees declined due to browsing pressure from moose (Thompson & Mallik 1988; Thompson & Curran 1993). In addition, a number of studies have demonstrated the effect of ungulates on soil nutrient processes (Wardle et al. 2001; Ayres et al. 2004; Carline & Bardgett 2005) and litter decomposition (Stark et al. 2000; Wardle et al. 2002; Bardgett & Wardle 2003; Haynes et al. 2014).

On Newfoundland, it seems that moose have directly affected plant recruitment and biomass production with no indication of indirect effects on soil ecosystems. The direct effects of moose on plant height and biomass can lead to some important

implications for other trophic levels. For example, researchers have found some evidence of cascading effects to other trophic levels on the island that might be related to plant species recruitment to the canopy. Rae et al. (2013) found evidence that black-throated warblers (*Setophaga virens*) and boreal chickadee (*Poecile hudsonicus*), forest specialist and generalist species respectively, were negatively associated with moose density. At the same time, bird species that preferred early successional forests, such as mourning warbler (*Geothlypis philadelphia*), increased in abundance in habitat where regeneration was impaired by moose (Rae et al. 2013). Tabuchi et al. (2011) found that abundance of a herbivorous insect (*Paradiplosis tumifex*) and its natural predator (*Dasineura balsamicola*) were reduced in areas of moose browsing as a result of shorter balsam fir shoot lengths. In Alberta, Canada, Teichman et al. (2013) found that browsing by ungulate reduced shrub cover of chokecherry (*Prunus virginiana*), an important cover species for yellow warbler (*Dendroica petechia*).

These direct effects of browsing ungulates may be a general pattern found across ecosystems. For example, Bressette et al. (2012) found that deer exclusion in oak-hickory forests in Virginia, USA increased the density of shrubs. Niwa et al. (2011) found sika deer in temperate forests of Japan reduced cover of dwarf bamboo. In addition, both studies found evidence of indirect effects on soil nutrients (Bressette et al. 2012) and soil microbial biomass (Niwa et al. 2011). However, I found this trend of indirect moose effects does not hold true on forest ecosystems I studied in Newfoundland, Canada. I can offer two potential explanations for why our study results differentiate from other studies of moose on forest ecosystems. Disturbance regime and soil properties explained a large portion of the variance in soil quality and litter decomposition rates. Differences in abiotic

conditions between disturbance regimes may be a more important predictor of nutrient processing in Newfoundland, Canada. Newfoundland has a marine climate with a short growing season. On average, between 70 to 90 days a year reach a minimum daily temperature of 10°C (Government of Canada 2015) limiting the ability of plants to grow. In addition, the exclosures in Newfoundland are approximately 20 years old. While the studies by Bressette et al. (2012) and Niwa et al. (2011) used exclosures of similar age to my study, coupled with the climate of Newfoundland may slow successional turnover within the exclosures.

### **3.2. Limitations and future direction**

Many studies that examine the effects of browsers on forest ecosystems are able to elucidate both direct and indirect effects. For example, Carline et al. (2005) found that red deer influenced the availability of nitrogen and phosphorus to soils and consequently limited the uptake of those elements to roots. Most of these studies use exclosures to examine forest ecosystems with and without the presence of the study species. Studies in Alaska (Gouch et al. 2007; Kielland and Bryant 1998), Virginia, (Bressette et al. 2012), Isle Royale (McInnes et al. 1992; Pastor et al. 1998), Britain (Carline et al. 2005), Sweden (Persson et al. 2009), and New Zealand (Wardle et al. 2001) have continued to report indirect browser effects on soil ecosystems. My research however, did not find evidence to support indirect effects into soil ecosystems. As previously mentioned, I may not have observed indirect effects of moose given the age of exclosures in conjunction with the short growing season in Newfoundland. Successional turnover is slow on the island; Ellis (1960) indicated that the growth of conifer species is slow during the first ten to twenty

years, which is the approximate age of the exclosures used in my study. Research conducted on Isle Royale using 40 year old exclosures found moose indirectly affected soil chemistry (McInnes et al. 1992). Further studies in Newfoundland should be conducted when the exclosures are approximately 30 – 40 years old to determine if indirect moose effects are influenced by timing of succession.

Soil fauna are an important component in nutrient cycling and litter decomposition. Research has demonstrated that ungulates can indirectly influence soil fauna which may have far researching implications for key ecosystem processes. For example, Niwa et al. (2010) found that soil microbial biomass was reduced in areas where sika deer were browsing in temperate forests of Japan. Wardle et al. (2001) demonstrated ungulate effects on invertebrate diversity in New Zealand. Mysterud et al. (2010) found that herbivorous beetles were negatively affected by high sheep density in Norway. My study did not examine the differences in invertebrate communities between moose exclosures and controls. Additional research in Newfoundland should examine the diversity of soil biota in moose exclosures and controls to determine if moose are affecting soil fauna in the province.

### **3.3. Implications for moose management in Newfoundland**

Parks Canada is concerned with the large moose population in Newfoundland, Canada as they have detected moose effects on forest regeneration and are concerned that the ecological integrity of the forests may be compromised as a result (Parks Canada 2013). Indeed, in other systems moose have directly and indirectly impacted the boreal forest (McInnes et al. 1992; Molvar et al. 1993; Kielland & Bryant 1998). My research found



that moose directly influence plant height and plant litter biomass but I did not find a moose effect on plant diversity, soil chemistry, or litter decomposition rates. Both Gros Morne (GMNP) and Terra Nova National Parks (TNNP) have implemented moose hunts within the parks since 2011. Parks Canada should continue to issue moose hunting tags in GMNP and TNNP to limit the moose population and allow for tree and shrub regeneration. While I did not find an indirect effect of moose on soil nutrient content or plant litter decomposition, over time, soil chemistry may change under high moose densities. Parks Canada should continue to monitor moose exclosures and references to determine if nutrient cycling is impacted over time.

### **3.4. References**

- Asner, G.P., S.R. Levick. 2012. Landscape-scale effects of herbivores on treefall in African savannas. *Ecology Letters* **15**: 1211 – 1217
- Ayres, E., J. Heath, M. Possell, H.I.J. Black, G. Kerstiens, R.D. Bardgett. 2004. Tree physiological responses to above-ground herbivory directly modify below-ground processes of soil carbon and nitrogen cycling. *Ecology Letters* **7**: 469 - 479
- Bardgett, R.D., D.A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* **84(9)**: 2258 - 2268
- Brandner, T.A., R.O. Peterson, K.L. Risenhoover. 1990. Balsam fir on Isle Royale: Effects of moose herbivory and population density. *Ecology* **71(1)**: 155 - 164
- Bressette, J.W., H. Beck, V.B. Beauchamp. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. *Oikos* **121**: 1749 - 1760

- Carline, K.A., H.E. Jones, R.D. Bardgett. 2005. Large herbivores affect the stoichiometry of nutrients in a regenerating woodland ecosystem. *Oikos* **110**: 453 – 460
- Carline, K.A., R.D. Bardgett. 2005. Changes in tree growth resulting from simulated browsing have limited effects on soil biological properties. *Soil Biology & Biochemistry* **37**: 2306 - 2314
- Ellis, R.C. 1960. Final report: An investigation of the length of regeneration period and of the yield potential of pulpwood cut-overs in Newfoundland. Department of Northern Affairs and National Resources Forestry Branch. Project NF 47. St. John's, Newfoundland
- Gough, L., E.A. Ramsey, D.R. Johnson. 2007. Plant-herbivore interactions in Alaskan arctic tundra change with soil nutrient availability. *Oikos* **116**: 407 - 418
- Government of Canada. 2015. Newfoundland and Labrador – Weather Conditions and Forecast by Locations. <  
[https://weather.gc.ca/forecast/canada/index\\_e.html?id=NL](https://weather.gc.ca/forecast/canada/index_e.html?id=NL)>
- Haynes, A.G., M. Schutz, N. Buchmann, D.S. Page-Dumroese, M.D. Busse, A.C. Risch. 2014. Linkages between grazing history and herbivore exclusion on decomposition rates in mineral soils of subalpine grasslands. *Plant Soil* **374**: 579 - 591
- Kielland, K., J.P. Bryant. 1998. Moose herbivory in Taiga: Effects of biogeochemistry and vegetation dynamics in primary succession. *Oikos* **82(2)**: 377 - 383
- Mason, N.W.H., D.A. Peltzer, S.J. Richardson, P.J. Bellingham, R.B. Allen. 2010. Stand development moderates effects of ungulate exclusion on foliar traits in the forests of New Zealand. *Journal of Ecology* **98**: 1422 – 1433

- Mathisen, K.M., F. Buhtz, K. Danell, R. Bergström, C. Skarpe, O. Suominen, I.L. Persson. 2010. Moose density and habitat productivity affects reproduction, growth and species composition in field layer vegetation. *Journal of Vegetation Science* **21**: 705 – 716
- McInnes, P.F., R.J. Naiman, J. Pastor, Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* **73**: 2059 – 2075
- Molvar, E.M., R.T. Bowyer, V. van Ballenberghe. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. *Oecologia* **94**: 472 - 479
- Mysterud, A., R. Aaserud, L.O. Hansen, K. Åkra, S. Olberg, G. Austrheim. 2010. Large herbivore grazing and invertebrates in an alpine ecosystem. *Basic and Applied Ecology* **11**(4): 320 – 328
- Niwa, S., L. Mariani, N. Kaneko, H. Okada, K. Sakamoto. 2011. Early-stage impacts of sika deer on structure and function of the soil microbial food webs in a temperate forest: A large-scale experiment. *Forest Ecology and Management* **261**: 391 - 399
- Parks Canada. 2013. Forest Health in Terra Nova National Park. <  
<http://www.pc.gc.ca/eng/progs/np-pn/sf-fh/terranova/lgde-sm.aspx>>
- Pastor, J., B. Dewey, R. Moen, D.J. Mladenoff, M. White, Y. Cohen. 1998. Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA. *Ecological Applications* **8**(2): 411 - 424

- Persson, I.L., M.B. Nilsson, J. Pastor, T. Eriksson, R. Bergstrom. 2009. Depression of belowground respiration rates at simulated high moose population densities in boreal forests. *Ecology* **90**(10): 2724 - 2733
- Rae, L.F., D.M. Whitaker, I.G. Warkentin. 2013. Multiscale impacts of forest degradation through browsing by hyperabundant moose (*Alces alces*) on songbird assemblages. *Diversity and Distributions* DOI: 10.1111/ddi.12133
- Stark, S., D.A. Wardle, R. Ohtonen, T. Helle, G.W. Yeates. 2000. The effect of reindeer grazing on decomposition, mineralization and soil biota in a dry oligotrophic Scots pine forest. *Oikos* **90**(2):301 - 310
- Suzuki, M., E. Ito. 2014. Combined effects of gap creation and deer exclusion on restoration of belowground systems of secondary woodlands: A field experiment in warm-temperate monsoon Asia. *Forest Ecology and Management* **329**: 227 - 236
- Tabuchi, K., D.T. Quiring, L.E. Flaherty, L.L. Pinault, K. Ozaki. 2011. Bottom-up trophic cascades caused by moose browsing on a natural enemy of galling insect on balsam fir. *Basic and Applied Ecology* **12**: 523 - 531
- Teichman, K.J., S.E. Nielsen, J. Roland. 2013. Trophic cascades: linking ungulates to shrub-dependent birds and butterflies. *Journal of Animal Ecology* **82**: 1288 – 1299
- Thompson, I.D., A.U. Mallik. 1989. Moose browsing and allelopathic of *Kalmia angustifolia* on balsam fir regeneration in central Newfoundland. *Canadian Journal of Forest Research* **19**: 524 - 526
- Thompson, I.D., W.J. Curran. 1993. A re-examination of moose damage to balsam fir - white birch forests in central Newfoundland: 27 years later. *Canadian Journal of Forest Research* **23**: 1388 - 1395

Thompson, I.D., W.J. Curran, J.A. Hancock, C.E. Butler. 1992. Influence of moose browsing on successional forest growth on black spruce sites in Newfoundland.

Forest Ecology and Management **47**: 29 – 37

Wardle, D.A., G.M. Barker, G.W. Yeates, K.I. Bonner, A. Ghani. 2001. Introduced

browsing mammals in New Zealand natural forests: Aboveground and belowground

consequences. Ecological Monographs **71(4)**: 587 – 614

Wardle, D.A., K.I. Bonner, G.M. Barker. 2002. Linkages between plant litter

decomposition, litter quality, and vegetation responses to herbivores. Functional

Ecology **16(5)**: 585 - 595

## Appendix I

**Table A. 1:** Matrix of plant composition hypotheses relatedness. Primary indicates the hypothesis being examined. Secondary refers to the hypothesis that relates to the primary hypothesis.

		Secondary			
		A.	B.	C.	D.
Primary	A.	X	Diversity will be dependent on species.	Diversity will be dependent on the number of individuals.	
	B.	Diversity will be dependent on species.	X	The number of individuals will be dependent on species.	
	C.	Diversity will be dependent on the number of individuals.	The number of individuals will be dependent on species.	X	The number of individuals may be dependent on the height of individuals.
	D.		Height of individuals will be dependent on species (preferred/non-preferred).	The number of individuals may be dependent on the height of individuals.	X

**Table A. 2:** Species preference definitions as found in Pimlott (), Dodds, and Tanner and Leroux (2014). Species not defined in these papers were assumed to be non-preferred plant species.

Preferred species	Non-preferred species
American green alder ( <i>Alnus viridis</i> )	Black spruce ( <i>Picea mariana</i> )
Balsam fir ( <i>Abies balsamea</i> )	Chokecherry ( <i>Prunus virginiana</i> )
Canadian yew ( <i>Taxus canadensis</i> )	European mountain ash ( <i>Sorbus aucuparia</i> )
Mountain ash ( <i>Sorbus aucuparia</i> )	Fern species
Mountain maple ( <i>Acer spicatum</i> )	Labrador tea ( <i>Rhododendron groenlandicum</i> )
Northern wild raisin ( <i>Viburnum cassinoides</i> )	Low bush blueberry ( <i>Vaccinium angustifolium</i> )
Pin cherry ( <i>Prunus pensylvanica</i> )	Mountain holly ( <i>Ilex mucronata</i> )
Red maple ( <i>Acer rubrum</i> )	Northern bush honeysuckle ( <i>Diervilla lonicera</i> )
Service berry ( <i>Amelanchier</i> sp.)	Sheep laurel ( <i>Kalmia angustifolia</i> )
Squash berry ( <i>Viburnum edule</i> )	Shining rose ( <i>Rosa nitida</i> )
White birch ( <i>Betula papyrifera</i> )	Swamp red currant ( <i>Ribes triste</i> )
	Tamarack ( <i>Larix laricina</i> )
	Wild raspberry ( <i>Rubus idaeus</i> )

**Table A. 3:** Dates of field work. Initial field work for Blue Hill centre control was performed on 09/08/2014 and was the only control performed on a different day than the adjacent moose enclosure.

Site	Initial Field Work	First collection date	Second collection date	Final collection date
Blue Hill centre	08/08/2014	18/08/2014	10/10/2014	08/11/2014
Blue Hill edge	08/08/2014	18/08/2014	10/10/2014	08/11/2014
Blue Hill West	07/08/2014	18/08/2014	10/10/2014	08/11/2014
Ochre Hill	06/08/2014	18/08/2014	10/10/2014	08/11/2014
Platter's Cove	04/08/2014	18/08/2014	10/10/2014	08/11/2014
Fox Marsh 1	11/08/2014	16/08/2014	11/10/2014	09/11/2014
Fox Marsh 2	12/08/2014	16/08/2014	11/10/2014	09/11/2014
Port Blandford centre	01/08/2014	18/08/2014	10/10/2014	08/11/2014
Port Blandford edge	02/08/2014	18/08/2014	10/10/2014	08/11/2014
Thorburn Lake	03/08/2014	18/08/2014	10/10/2014	09/11/2014



**Table A. 4:** Summary table of decomposition bag contents lost either in the field due to herbivory or lost in the muffle furnace during the drying process. (Time 1 represents the period of time after 35 – 47 days, Time 2 represents the period of time after 61 – 70 days, Time 3 represents the period of time after 89 – 98 days)

Sample	Reason of Loss	Date	Location
Litter decomposition bag	Herbivory	Time 1	Blue Hill centre exclosure, Fox Marsh 1 control, Port Blandford centre exclosure (2)
		Time 2	Platter's Cove control, Port Blandford edge exclosure
		Time 3	Blue Hill edge control, Port Blandford edge exclosure
	Muffle furnace	For days 36 – 47	Blue Hill centre control, Blue Hill edge control, Blue Hill West exclosure, Blue Hill West control, Ochre Hill exclosure, Ochre Hill control (2), Thorburn Lake exclosure, Thorburn Lake control

**Table A. 5:** Mean values of % C, % N, and % P in four species found in at least one paired exclosure and control site. Samples of balsam fir were homogenized within site. Samples of black spruce and white birch were homogenized across the study area. Red maple was only present in one exclosure/control location but the control material was <0.100gm and could not be analyzed for carbon, nitrogen, or phosphorus. Mean values were compared between exclosure and control (E-X), exclosure and homogenized (E-H), and control and homogenized (X-H). A negative value indicates the direction of the difference.

		<i>Abies balsamea</i>	<i>Acer rubrum</i>	<i>Betula papyrifera</i>	<i>Picea mariana</i>
% Carbon	Exclosure	54.11	50.1	51.68	52.63
	Control	55.7	na	51.7	53.6
	Homogenized	54.63	50.6	52.2	53.7
	E-X	-1.59	na	-0.025	-0.98
	E-H	-0.52	-0.5	-0.525	-1.08
	X-H	1.07	na	-0.5	-0.1
% Nitrogen	Exclosure	0.72	0.44	0.87	0.50
	Control	0.69	na	0.86	0.51
	Homogenized	0.69	0.44	0.70	0.63
	E-C	0.026	na	0.01	-0.013
	E-H	0.022	0	0.18	-0.14
	C-H	-0.0033	na	0.17	-0.12
% Phosphorus	Exclosure	0.053	0.045	0.066	0.032
	Control	0.057	na	0.064	0.043
	Homogenized	0.051	0.027	0.045	0.055
	E-C	-0.0040	na	0.0015	-0.010
	E-H	0.0027	0.018	0.02	-0.022
	C-H	0.0067	na	0.020	-0.012

**Table A. 6:** Summary of mass of species obtained at sites. Species are categorized by elements obtained for analysis. Species samples that had >0.500 gm of material were analyzed for all 11 elements (C, N, P, K, Ca, Mg, Fe, Cu, Mn, Zn, B). Species samples that had <0.320 gm of material were analyzed for 9 of 11 elements (P, K, Ca, Mg, Fe, Cu, Mn, Zn, B). Species samples that had <0.100 gm of material could not be analyzed for any elements. Seeds/cones and wood were not sent for analysis.

Site	>0.500gm			<0.320gm			<0.100gm		
	Species	Count	Weight	Species	Count	Weight	Species	Count	Weight
Blue Hill centre exclosure	<i>Acer rubrum</i>	16	1.63g				<i>Cornus sericea</i>	3	0.076 g
	<i>Picea mariana</i>	102	0.21 g				<i>Cornus canadensis</i>	1	0.02 g
	<i>Abies balsamea</i>	52	0.099 g				Seeds/cones	54	0.39 g
	<i>Populus tremuloides</i>	12	1.28 g				Wood	18	0.33 g
	<i>Prunus pensylvanica</i>	57	1.23 g						
	<i>Prunus virginiana</i>	4	0.19 g						
	<i>Amelanchier</i> sp.	14	0.27 g						
	<i>Betula papyrifera</i>	132	11.54 g						
	<i>Solidago canadensis</i>	1	0.015 g						
	Fern sp.	3	0.016 g						
Blue Hill edge exclosure	<i>Kalmia angustifolia</i>	147	4.01 g	<i>Ilex mucronata</i>	2	0.016 g	<i>Vaccinium angustifolium</i>	30	0.16 g
	<i>Acer rubrum</i>	22	3.28 g				<i>Viburnum nudum</i>	3	0.10 g
	<i>Betula papyrifera</i>	158	15.37 g				Seeds/cones	144	4.54 g
	<i>Abies balsamea</i>	77	0.12 g				Wood	45	1.75 g
	<i>Picea mariana</i>	~3178	6.17 g						
	<i>Amelanchier</i> sp.	38	0.80 g						
	<i>Populus tremuloides</i>	12	1.76 g						
Blue Hill West exclosure	<i>Kalmia angustifolia</i>	8	0.16 g	<i>Ilex mucronata</i>	8	0.13 g	Seeds/cones	78	0.44 g
	<i>Picea mariana</i>	~6940	12.33 g						
Ochre Hill	<i>Larix laricina</i>	332	0.23 g						
	<i>Prunus pensylvanica</i>	10	0.19 g				<i>Cornus canadensis</i>	1	0.022 g

exclosure	<i>Solidago canadensis</i>	5	0.021 g			Seeds/cones	114	0.46 g	
	<i>Amelanchier</i> sp.	7	0.14 g			Wood	22	0.35 g	
	<i>Kalmia angustifolia</i>	241	5.023 g						
	<i>Betula papyrifera</i>	194	18.32 g						
	Fern sp.	39	0.66 g						
	<i>Abies balsamea</i>	845	2.68 g						
	<i>Picea mariana</i>	24	0.038 g						
Platter's Cove exclosure	<i>Alnus viridis</i>	73	9.12 g	<i>Ilex mucronata</i>	1	0.006 g	<i>Ribes triste</i>	2	0.11 g
	<i>Picea mariana</i>	~7222	7.95 g				Seeds/cones	161	2.27 g
	<i>Populus tremuloides</i>	37	4.50 g				Wood	76	2.82 g
	<i>Betula papyrifera</i>	145	17.39 g						
	<i>Abies balsamea</i>	1308	5.17 g						
Fox Marsh 1 exclosure	Fern sp.	1	0.016 g				Seeds/cones	69	0.38 g
	<i>Abies balsamea</i>	~11,643	28.39 g				Wood	29	0.18 g
	<i>Amelanchier</i> sp.	24	0.53 g						
	<i>Prunus pensylvanica</i>	35	0.14 g						
	<i>Betula papyrifera</i>	14	0.22 g						
Fox Marsh 2 exclosure	<i>Betula papyrifera</i>	5	0.13 g				<i>Cornus canadensis</i>	1	0.017 g
	<i>Amelanchier</i> sp.	10	0.27 g				Seeds/cones	86	0.79 g
	<i>Prunus pensylvanica</i>	4	0.11 g				Wood	23	0.36 g
	<i>Abies balsamea</i>	~28,868	56.84 g						
Port Blandford centre exclosure	<i>Prunus pensylvanica</i>	2	0.099 g				<i>Vaccinium angustifolium</i>	1	0.066 g
	<i>Amelanchier</i> sp.	6	0.17 g				Seeds/cones	69	1.69 g
	<i>Abies balsamea</i>	~5311	12.57 g				Wood	28	0.17 g
	<i>Picea mariana</i>	671	1.032 g						
	<i>Kalmia angustifolia</i>	64	1.92 g						
	<i>Betula papyrifera</i>	21	1.03 g						
Port Blandford edge exclosure	<i>Betula papyrifera</i>	82	7.47 g	<i>Ilex mucronata</i>	1	0.014 g	Seeds/cones	87	0.52 g
	<i>Kalmia angustifolia</i>	316	8.17 g				Wood	7	0.14 g
	<i>Abies balsamea</i>	1260	4.48 g						
	<i>Picea mariana</i>	~3093	3.81 g						
	<i>Larix laricina</i>	656	0.31 g						

	<i>Prunus pensylvanica</i>	5	0.085 g						
	<i>Alnus viridis</i>	5	0.64 g						
	<i>Prunus pensylvanica</i>	84	2.54 g	<i>Sorbus aucuparia</i>	18	0.40 g	<i>Viburnum nudum</i>	6	0.20 g
	<i>Abies balsamea</i>	1750	5.07 g	<i>Ilex mucronata</i>	27	0.27 g	Seeds/cones	121	1.07 g
	<i>Betula papyrifera</i>	290	30.56 g				Wood	45	1.78 g
Thorburn Lake enclosure	<i>Amelanchier</i> sp.	88	3.01 g						
	<i>Prunus virginiana</i>	13	0.56 g						
	<i>Acer spicatum</i>	42	3.80 g						
	<i>Larix laricina</i>	502	0.27 g						
	<i>Alnus viridis</i>	110	10.43 g						
	<i>Picea mariana</i>	85	0.17 g						
	<i>Populus tremuloides</i>	32	3.19 g						
Blue Hill centre control	<i>Acer rubrum</i>	1	0.28 g				Grass sp.	1	0.014 g
	<i>Solidago canadensis</i>	15	0.16 g				<i>Chamerion angustifolium</i>	3	0.011 g
	<i>Betula papyrifera</i>	6	0.54 g				Seeds/cones	8	0.009 g
	<i>Abies balsamea</i>	16	0.02 g				Wood	2	0.035 g
Blue Hill edge control	<i>Abies balsamea</i>	1	0.005 g				Grass sp.	2	0.01 g
	<i>Prunus pensylvanica</i>	1	0.01 g				Seeds/cones	9	0.021 g
	<i>Alnus viridis</i>	58	6.92 g				Wood	6	0.14 g
	<i>Picea mariana</i>	258	0.69 g						
	<i>Solidago canadensis</i>	14	0.31 g						
Blue Hill West control	<i>Abies balsamea</i>	269	0.37 g				Seeds/cones	37	0.10 g
	<i>Picea mariana</i>	1388	2.09 g				Wood	17	1.01 g
	<i>Kalmia angustifolia</i>	90	1.78 g						
Ochre Hill control	Fern sp.	49	2.77 g				<i>Vaccinium angustifolium</i>	1	0.013 g
	<i>Picea mariana</i>	72	0.12 g				Seeds/cones	26	0.07 g
	<i>Abies balsamea</i>	117	0.27 g				Wood	7	0.035 g
	<i>Betula papyrifera</i>	5	0.42 g						
Platter's Cove control	<i>Solidago canadensis</i>	1	0.012 g						
	<i>Alnus viridis</i>	6	1.18 g						
	<i>Abies balsamea</i>	171	0.62 g						
	<i>Rubus idaeus</i>	32	1.23 g						
	<i>Betula papyrifera</i>	545	53.49 g						

Fox Marsh 1 control	<i>Abies balsamea</i>	1070	2.05 g			Seeds/cones	85	0.21 g	
	<i>Rubus idaeus</i>	19	0.58 g			Wood	9	0.074 g	
	<i>Solidago canadensis</i>	50	0.96 g						
	<i>Eurybia spectabilis</i>	35	0.81 g						
Fox Marsh 2 control	<i>Abies balsamea</i>	~23,12 9	39.77 g			Seeds/cones	31	0.095 g	
						Wood	20	0.41 g	
Port	<i>Kalmia angustifolia</i>	41	0.55 g			Seeds/cones	3	0.007 g	
Blandford centre control	<i>Abies balsamea</i>	53	0.057 g			Wood	8	0.11 g	
	<i>Picea mariana</i>	78	0.073 g						
Port Blandford edge control	<i>Acer rubrum</i>	1	0.10 g	<i>Sorbus aucuparia</i>	1	0.031 g	Seeds/cones	15	0.055 g
	<i>Prunus pensylvanica</i>	3	0.032 g						
	<i>Amelanchier</i> sp.	10	0.38 g						
	<i>Larix laricina</i>	247	0.16 g						
	<i>Abies balsamea</i>	756	1.88 g						
	<i>Picea mariana</i>	94	0.15 g						
Thorburn Lake control	<i>Betula papyrifera</i>	16	1.04 g	<i>Sorbus aucuparia</i>	5	0.065 g	Grass sp.	6	0.088 g
	<i>Kalmia angustifolia</i>	3	0.056 g				Seeds/cones	45	0.088 g
	<i>Solidago canadensis</i>	20	0.23 g				Wood	3	0.004 g
	<i>Larix laricina</i>	1121	0.56 g						
	<i>Abies balsamea</i>	113	0.24 g						

**Table A. 7:** Summary of plant species diversity as measured by Shannon Wiener index and Simpson diversity index between moose exclosure and control.

Site	Exclosure/Control	Shannon Wiener index	Simpson diversity
Blue Hill centre	Exclosure	1.89	0.82
	Control	1.32	0.69
Blue Hill edge	Exclosure	1.86	0.81
	Control	2.12	0.85
Blue Hill West	Exclosure	0.96	0.46
	Control	1.15	0.54
Ochre Hill	Exclosure	1.43	0.69
	Control	1.40	0.67
Platter's Cove	Exclosure	1.52	0.73
	Control	0.68	0.33
Fox Marsh 1	Exclosure	1.49	0.73
	Control	0.78	0.40
Fox Marsh 2	Exclosure	0.18	0.08
	Control	0.14	0.06
Port Blandford centre	Exclosure	1.45	0.74
	Control	1.22	0.60
Port Blandford edge	Exclosure	1.14	0.62
	Control	1.67	0.78
Thorburn Lake	Exclosure	1.51	0.72
	Control	2.19	0.88

**Table A. 8:** Two general linear mixed effects models to determine how the Simpson diversity index is affected by exclosure/control, and site nested in disturbance regime.

Model	Description	k	LL	$\Delta AIC_c$	$\omega AIC_c$	Marginal $R^2$	Conditional $R^2$
1	1 + (1 Disturbance regime/Site)	4	-14.48	0.00	0.93	na	0.70
2	Exclosure/Control + (1 Disturbance regime/Site)	5	-15.28	5.22	0.069	0.016	0.70

k, number of parameters; LL, log-likelihood;  $AIC_c$ , Akaike information criterion,  $\Delta AIC_c$ ,

difference in AIC between most parsimonious model and subsequent models;  $\omega AIC_c$ ,

Weight of models



**Table A. 9:** Summary of mixed effects models to determine how plant community composition is affected by exclosure/control, and site nested in disturbance regime. I used 8 different response variables to tests for these effects. Models are listed by their  $\Delta AICc$  value.

Response	Fixed Effects	Parameter Estimates		
		Estimate	Standard Error	t value
Shannon Wiener Index	Model 1 ~ 1 + (1 disturbance regime/site)			
	Intercept	1.28	0.20	6.29
	Model 2 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	1.24	0.22	5.68
	Exclosure	0.068	0.16	0.42
Simpson Index	Model 1 ~ 1 + (1 disturbance regime/site)			
	Intercept	0.59	0.088	6.79
	Model 2 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	0.57	0.093	6.088
Number of preferred species	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	3.50	0.76	4.6
	Exclosure	0.00	0.60	0.0
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	3.50	0.70	5.00
Number of non-preferred species	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	3.00	0.30	10.03
	Exclosure	-0.11	0.39	-0.29
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	2.94	0.27	12.95
Number of preferred individuals	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	36.90	9.24	3.99
	Exclosure	-1.70	11.45	-0.15
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	36.05	7.25	4.97
Number of non-preferred individuals	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	70.25	16.71	4.21
	Exclosure	-35.11	19.51	-1.80
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	52.22	13.53	3.86
Height of preferred individuals	Model 1 ~ exclosure/control + (1 disturbance regime/site))			
	Intercept	72.82	11.45	6.36
	Exclosure	43.27	4.63	9.35
	Model 2 ~ 1 + (1 disturbance regime/site))			

	Intercept	92.48	12.65	7.31
	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	61.33	4.38	14.01
	Exclosure	19.14	2.09	9.15
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	69.46	5.37	12.94
	Exclosure	0.061	0.061	1.010

**Table A. 10:** Summary of mixed effects models to determine how plant litter quantity is affected by exclosure/control, and site nested in disturbance regime. I used 6 different response variables to tests for these effects. Models are listed by their  $\Delta\text{AICc}$  value.

Response	Fixed Effects	Parameter Estimates		
		Estimate	Standard Error	t value
Litter biomass	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	1.64	0.34	4.82
	Exclosure	1.84	0.36	5.05
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	2.54	0.31	8.24
Mass of carbon	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	-1.57	0.35	-4.49
	Exclosure	1.85	0.38	4.83
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	-0.65	0.32	-2.05
Mass of nitrogen	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	-5.81	0.39	-14.84
	Exclosure	1.65	0.42	3.98
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	-4.99	0.34	-14.87
Mass of phosphorus	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Exclosure	-9.29	0.40	-23.43
	Intercept	1.67	0.41	4.075
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	-8.46	0.35	-24.47
C:N Ratio	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	75.23	6.73	11.18
	Exclosure	11.23	9.44	1.19
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	80.84	4.81	16.82
N:P Ratio	Model 1 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	33.19	2.04	16.26
	Exclosure	-1.05	2.61	-0.40
	Model 2 ~ 1 + (1 disturbance regime/site)			
	Intercept	32.66	1.57	20.8

**Table A. 11:** Summary of mixed effects models to determine how soil quality is affected by exclosure/control, and site nested in disturbance regime. I used 3 different response variables to tests for these effects. Models are lited by their  $\Delta AICc$  value.

Response	Fixed Effects	Parameter Estimates		
		Estimate	Standard Error	t value
% Carbon	Model 1 ~ exclosure/control + soil pH + soil moisture + soil depth + (1 disturbance regime/site)			
	Intercept	7.33	10.66	0.69
	Exclosure	0.71	1.70	0.42
	pH	-4.20	1.88	-2.23
	Soil moisture	88.90	10.05	8.85
	Soil depth	-0.65	0.29	-2.21
	Model 2 ~ exclosure/control + soil pH + soil moisture + (1 disturbance regime/site)			
	Intercept	1.64	10.60	0.16
	Exclosure	-0.72	1.59	-0.45
	pH	-3.51	1.90	-1.85
	Soil moisture	80.43	9.68	8.31
	Model 3 ~ exclosure/control + soil moisture + soil depth + (1 disturbance regime/site)			
	Intercept	-12.50	6.17	-2.03
	Exclosure	1.37	1.69	0.81
	Soil moisture	91.08	10.16	8.96
	Soil depth	-0.53	0.29	-1.81
	Model 4 ~ exclosure/control + soil moisture + (1 disturbance regime/site)			
	Intercept	-14.79	6.05	-2.44
	Exclosure	0.13	1.55	0.083
	Soil moisture	84.09	9.59	8.77
	Model 5 ~ exclosure/control + pH + (1 disturbance regime/site)			
	Intercept	52.40	11.27	4.65
	Exclosure	-2.29	2.17	-1.06
	pH	-6.08	2.58	-2.35
	Model 6 ~ exclosure/control + soil depth + soil pH + (1 disturbance regime/site)			
	Intercept	45.39	13.02	3.49
	Exclosure	-3.11	2.30	-1.35
	Soil depth	0.42	0.39	1.06
	pH	-5.45	2.64	-2.06
	Model 7 ~ exclosure/control + (1 disturbance regime/site)			

% Nitrogen	Intercept	26.94	3.22	8.36
	Exclosure	-0.81	2.19	-0.37
	Model 8 ~ exclosure/control + soil depth + (1 disturbance regime/site)			
	Intercept	20.94	5.14	40.76
	Exclosure	-2.05	2.34	-0.88
	Soil depth	0.57	0.39	1.45
	Model 9 ~ 1 + (1 disturbance regime/site)			
	Intercept	26.53	3.03	8.76
	Model 1 ~ exclosure/control + soil moisture + (1 disturbance regime/site)			
	Intercept	-0.39	0.17	-2.29
	Exclosure	-0.10	0.043	-2.30
	Moisture	2.61	0.28	9.34
	Model 2 ~ exclosure/control + soil moisture + soil depth + (1 disturbance regime/site)			
	Intercept	-0.27	0.17	-1.60
	Exclosure	-0.035	0.046	-0.76
	Moisture	2.94	0.29	10.20
	Depth	-0.028	0.0085	-3.27
	Model 3 ~ exclosure/control + pH + soil moisture + (1 disturbance regime/site)			
	Intercept	-0.73	0.31	-2.40
	Exclosure	-0.088	0.045	-1.95
	pH	0.078	0.055	1.41
	Moisture	2.64	0.29	9.20
	Model 4 ~ exclosure/control + pH + soil moisture + soil depth + (1 disturbance regime/site)			
	Intercept	-0.56	0.30	-1.85
	Exclosure	-0.027	0.048	-0.56
	pH	0.065	0.054	1.21
	Moisture	2.96	0.30	10.00
	Depth	-0.027	0.0087	-3.06
	Model 5 ~ 1 + (1 disturbance regime/site)			
	Intercept	0.84	0.078	10.84
	Model 6 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	0.91	0.084	10.77
	Exclosure	-0.13	0.065	-1.99
	Model 7 ~ exclosure/control + pH + (1 disturbance regime/site)			
	Intercept	0.84	0.34	2.47
	Exclosure	-0.14	0.067	-2.02
	pH	0.015	0.079	0.20
	Model 8 ~ exclosure/control + soil depth + (1 disturbance			

% Phosphorus	regime/site)			
	Intercept	0.88	0.15	5.87
	Exclosure	-0.14	0.070	-1.93
	Soil depth	0.0030	0.012	0.25
	Model 9 ~ exclosure/control + soil depth + pH + (1 disturbance regime/site)			
	Intercept	0.77	0.40	1.94
	Exclosure	-0.14	0.071	-2.03
	Soil depth	0.0047	0.012	0.38
	pH	0.021	0.082	0.26
	Model 1 ~ 1 + (1 disturbance regime/site)			
	Intercept	0.0028	0.0005	5.09
	Model 2 ~ exclosure/control + (1 disturbance regime/site)			
	Intercept	0.0025	0.0006	4.22
	Exclosure	0.0001	0.0002	0.62
	Model 3 ~ exclosure/control + moisture + (1 disturbance regime/site)			
	Intercept	0.0016	0.0010	1.57
	Exclosure	0.0002	0.0002	0.71
	Moisture	0.0019	0.0016	1.22
	Model 4 ~ exclosure/control + soil depth + (1 disturbance regime/site)			
	Intercept	0.88	0.15	5.87
	Exclosure	-0.14	0.070	-1.93
	Soil depth	0.0030	0.012	0.25
	Model 5 ~ exclosure/control + pH + (1 disturbance regime/site)			
	Intercept	0.0012	0.0014	0.88
	Exclosure	0.0002	0.0002	0.63
	pH	0.003	0.0003	1.04
	Model 6 ~ exclosure/control + moisture + depth + (1 disturbance regime/site)			
	Intercept	2.13e-3	9.96e-4	2.14
	Exclosure	4.46e-4	2.64e-4	1.69
	Moisture	3.26e-3	1.65e-3	1.98
	Soil depth	-1.19e-4	4.91e-5	-2.43
	Model 7 ~ exclosure/control + pH + moisture + (1 disturbance regime/site)			
	Intercept	7.67e-5	1.72e-3	0.045
	Exclosure	1.91e-4	2.49e-4	0.77
	pH	3.68e-4	3.05e-4	1.21
	Moisture	1.84e-3	1.59e-3	1.16
	Model 8 ~ exclosure/control + soil depth + pH + (1 disturbance regime/site)			

Intercept	0.77	0.40	1.94
Exclosure	-0.14	0.071	-2.03
Soil depth	0.0047	0.012	0.38
pH	0.021	0.082	0.26
Model 9 ~ exclosure/control + pH + moisture + depth + (1 disturbance regime/site)			
Intercept	8.01e-4	1.73e-3	0.46
Exclosure	4.28e-4	2.70e-4	1.59
pH	3.10e-4	3.03e-4	1.02
Moisture	3.04e-3	1.67e-3	1.82
Soil depth	-1.04e-4	4.95e-5	-2.11

**Table A. 12:** Summary of the top three (out of 13) general linear mixed effects models to determine how mass remaining is affected by time, exclosure/control, and disturbance regime. Data was collected from August 1 to November 9, 2014.

Response	Fixed Effects	Parameter Estimates		
		Estimate	Standard Error	t value
Oven Dry Weight	Model 1 ~ time + (1 disturbance regime/site)			
	Intercept	0.50	0.089	5.68
	Time	-0.005	0.0008	-6.18
	Model 2 ~ time + soil moisture + (1 disturbance regime/site))			
	Intercept	0.509	0.14	3.63
	Time	-0.0050	0.0008	-6.16
	Moisture	-0.013	0.22	-0.058
	Model 3 ~ time + exclosure/control + (1 disturbance regime/site)			
	Intercept	0.52	0.090	5.79
	Time	-0.0050	0.0008	-6.16
	Exclosure	-0.040	0.034	-1.15
	Model 10 ~ 1 + (1 disturbance regime/site)			
	Intercept	0.17	0.074	2.27

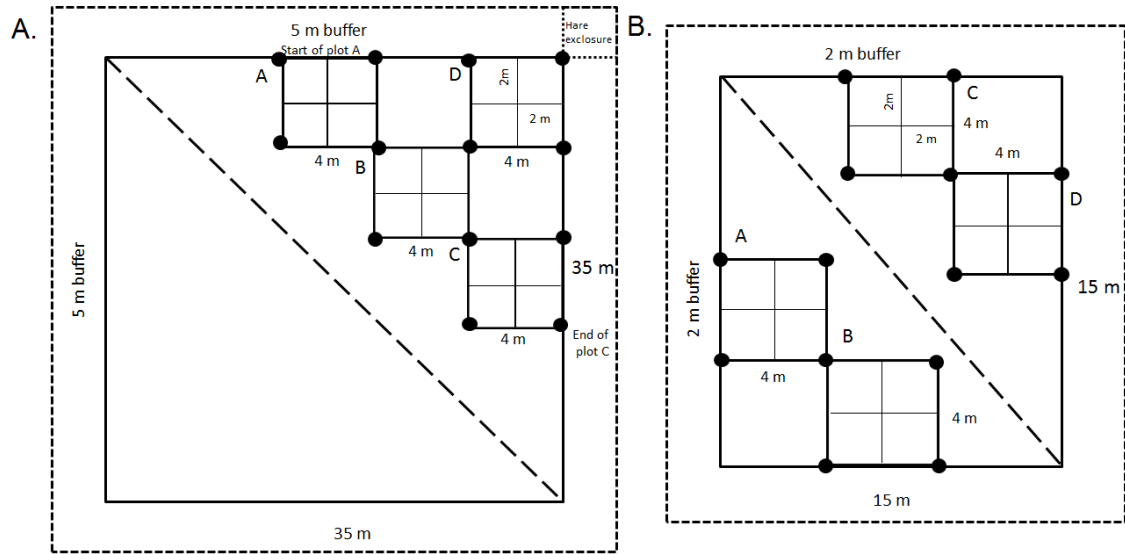


**Table A. 13:** Summary of studies examining moose effects on the boreal forest ecosystem of Isle Royale, USA.

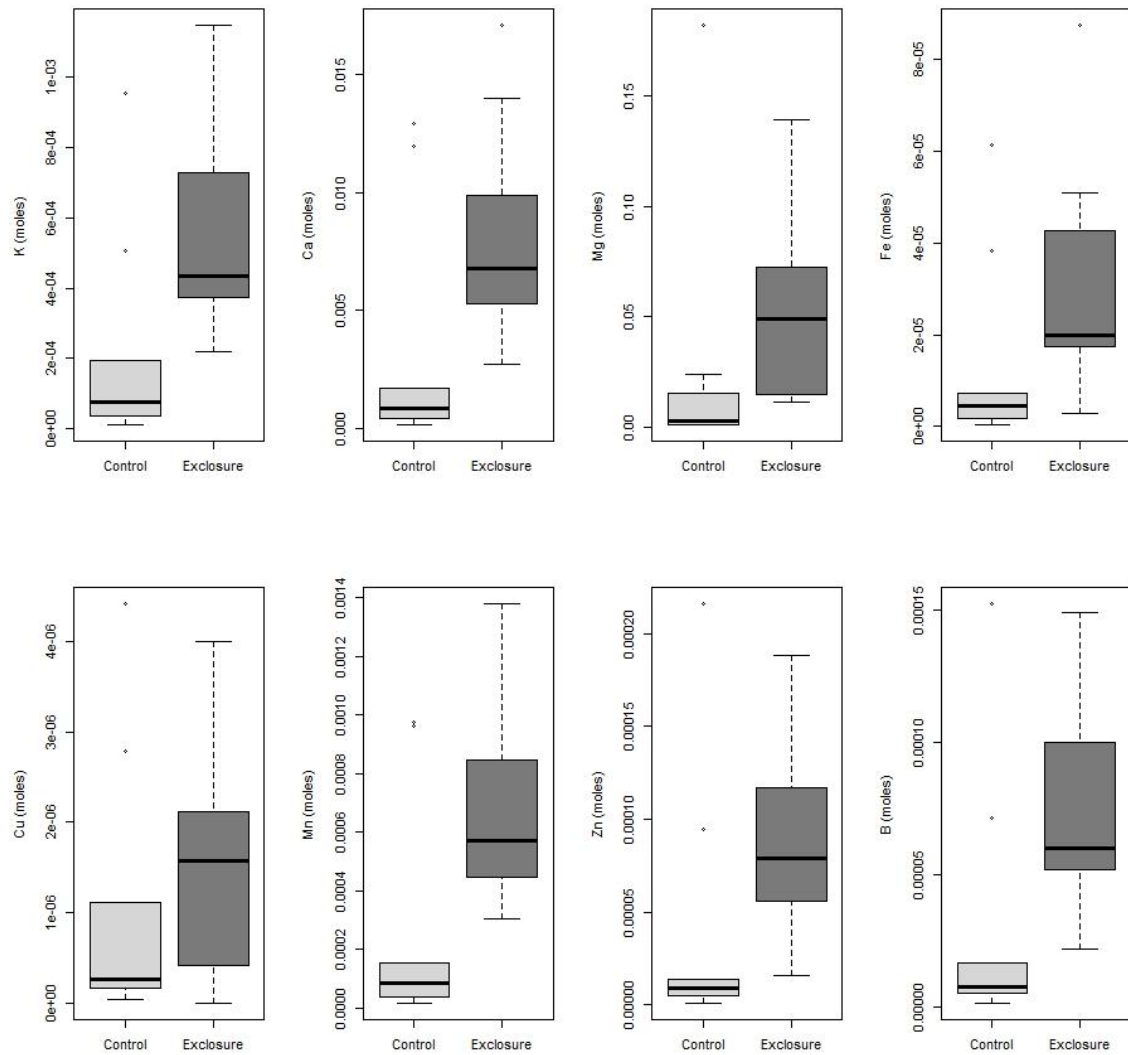
Authors	Time Frame of Study	Number of Sites	Abiotic environment	Moose density	Results found
Rotter, M.C. & A.J. Rebertus (2015)	Age of savanna (<10 years to 80 years)	Five age classes, 10 – 11 savannas chosen with 15 plots within each savanna	Heavily forested, no major fires, deeper soils		Lowest richness in reference area (86 species) and highest in 1930s age class (149); Forest species ( <i>Oxalis acetosella</i> , <i>Coptis trifolia</i> , <i>Huperzia lucidula</i> ) poorly represented in all savannas although more abundant in older age classes
Pastor, J., B. Dewey, R. Moen, D.J. Mladenoff, M. White, Y. Cohen (1998)	One year	In two valleys, 10 transects	No fires since the turn of the century in valleys	3.7 moose/km <sup>2</sup>	Smaller size classes of aspen present only where consumption is <4g/m <sup>2</sup> /year while smaller size classes are reduced where consumption is higher; high N availability only occurs in the absence of significant plant consumption of moose
Pastor, J., B. Dewey, R.J. Naiman, P.F. McInnes, Y. Cohen (1993)	Exclosures established between 1948 and 1950	Four exclosures/control plots	Forests on glacial till, large fires between 1936 and 1938 regenerated to aspen and paper birch,	2.8 moose/km <sup>2</sup>	Excluding moose significantly increased soil [Na, K, Mg] and cation exchange capacity at heavily browsed site (p<0.03, 0.00, 0.02, 0.02); excluding moose increased concentrations of total N by ~14% and C by ~20% above control levels (p < 0.02 for each); excluding moose significantly increased field N mineralization at most heavily browsed sites but not least heavily browsed sites (p<0.001)
McInnes, P.F., R.J. Naiman, J.	Exclosures established between	Four exclosures/control plots	Inland, high elevation sites support hardwood vegetation while low		The mean tree biomass was significantly higher in exclosures than browsed plots (p<0.05); mean density of trees in

Pastor, Y. Cohen (1992)	1948 and 1950		elevations close to Lake Superior support boreal plant species; snow depth varies from 0.5 to 1 m and average annual precipitation on the island is ~75 cm		exclosures was significantly greater than in the browsed plots ( $p < 0.05$ ); mean shrub biomass was significantly less than in browsed plots ( $p < 0.05$ ); mean herb biomass significantly lower in exclosure than browsed plot ( $p < 0.05$ ); mean litter fall in exclosures was greater than browsed plots ( $p < 0.05$ ); mean nutrient content of the tree and shrub litter for all sites was similar - mean C:N ratios of tree and shrub litter was not significantly different ( $p > 0.1$ ); absolute amounts of N and C in shrub and tree litter were significantly greater in exclosures than browsed plots ( $p < 0.05$ )
Brandner, T.A., R.O. Peterson, K.L. Risenhoover (1990)	Five years	Nine sites with different balsam fir stem densities (3 at low, 3 at medium, 3 at high)		Ranges from ~0.8 - ~5 moose /km <sup>2</sup>	At low fir density, all individuals exhibited height growth suppression even at low moose population density ( $p < 0.0001$ ). Similar trends were seen at medium fir density where 20% of saplings were never browsed at one site. High fir density sites showed evidence of past browse damage, was released from browse damage. Sapling heights differed significantly among fir density levels and moose density levels ( $p < 0.05$ )
Risenhoover, K.L, S.A. Maas (1986)	33 years browsing pressure	Four exclosure/control pairs	Annual precipitation averages 750 mm. Snow depth ranges between 0.5 and 1.0m.		Differences in forest structure between exclosure and control areas were significant ( $p$ ranged from $< 0.005$ to $< 0.01$ ). Repeated breakage or browsing of terminal growth seen while heights of plant species were greater in exclosure plots.

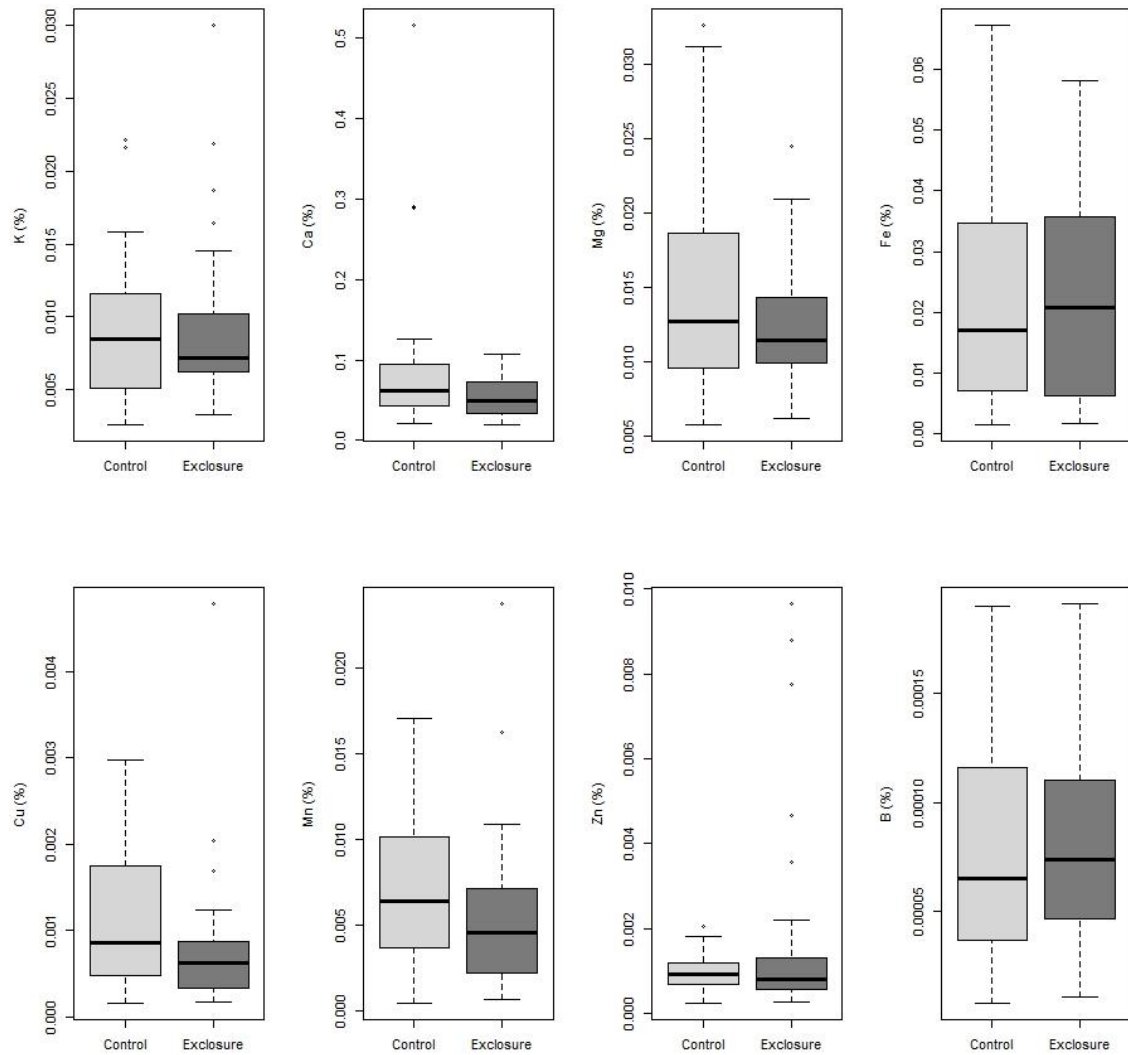
Snyder, J.D., R.A. Janke (1976)	Six sites	Precipitation averages 750 mm.	Total tree density show browsed sites have significantly lower values than unbrowsed sites ( $p<0.05$ ). No significant difference in total basal area between browsed and unbrowsed sites but average basal area per tree was significantly greater for browsed sites ( $p<0.05$ ). Balsam fir densities were lower in browsed than unbrowsed sites ( $p=0.7$ ). Browsed sites have significantly greater densities of white spruce than unbrowsed sites ( $p<0.01$ ).
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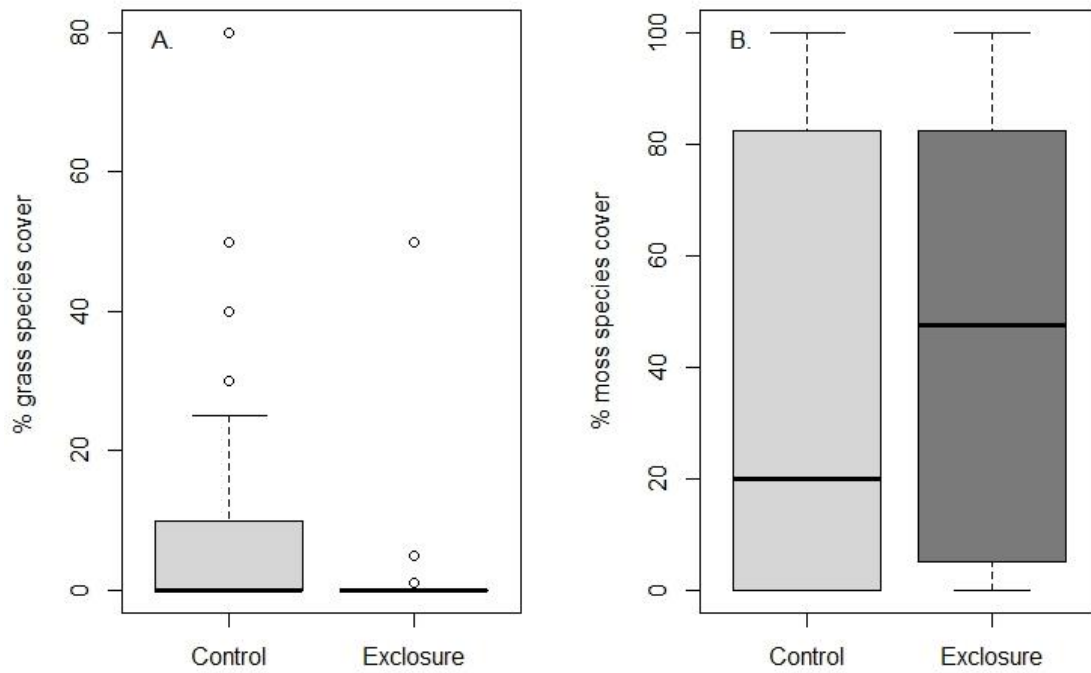
**Figure A. 1:** Exclosure-control layout for sites in a) Terra Nova National Park and in the Clarendville area and b) on the Avalon Peninsula. Four 4m x 4m plots were allocated to a corner of the exclosure. Each plot was then divided into four 2m x 2m subplots that were randomly selected for plant identification and as the location for litter fall traps. The adjacent control plots ran in the same direction as the plots established in the exclosure.



**Figure A. 2:** The molar mass (in moles) (top left to top right) potassium, calcium, magnesium, and iron and (bottom left to bottom right) copper, manganese, zinc, and boron found in plant litter fall in moose exclosures and controls.



**Figure A. 3:** The % (top left to top right) potassium, calcium, magnesium, and iron and (bottom left to bottom right) copper, manganese, zinc, and boron found in soils in moose exclosures and controls.



**Figure A. 4:** Comparison of A) % grass cover and moose exclosure/control; and B) % moss cover and moose exclosure/control. I found a positive correlation between % grass cover and control and no correlation between % moss cover and moose exclosure/control.